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THE PRIMROSE AND DARWINISM

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BY

A FIELD NATURALIST

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PREFACE

The views set forth in our initial chapters appeared in a shortened form as an Article in the London "Quarterly Review" for October, 1899. With the kind permission of the Editor of that Review, we have adopted any statements there made in the enlarged treatment of the subject in the present volume.

The evidence for the statements made in these pages is particularly and chiefly circumstantial evidence. We have, too, with some few exceptions, confined our observations to English wild flowers, since foreign plants removed from their natural habitats, where they are endemic, into our greenhouses and gardens, where atmospheric conditions, and very possibly the soil, are totally different, are very often greatly affected, and even in some cases fail altogether, in fertility. They consequently can give no reliable indication as to their natural fertility in their native soil.

The validity of the circumstantial evidence recorded in these pages can consequently be tested by any observer who is acquainted with our English wild flowers, and still more particularly by those who have also some acquaintance with our wild bees especially, and with other honey- and pollen-feeding insects.

Sir Joseph Hooker, at the inauguration of the Darwin statue at the Oxford University Museum on June 17th, 1899, said in his opening address that "when Darwin's now famous account of the two forms, or dimorphic condition,

of Primulas, for which Darwin took the common primrose as an illustration, was read years ago before the Linnæan Society, an enthusiastic admirer of its author got up and likened British botanists, who had overlooked so conspicuous and beautiful a contrivance to effect cross-fertilization, to Wordsworth's *Peter Bell*, of whom the poet wrote—

> 'A primrose by a river's brim
> A yellow primrose was to him,
> And it was nothing more.'"

We think that the enthusiasm of this admirer of Darwin caused him to cast upon the reputation of some of Darwin's English predecessors an unnecessary and unmerited slur. The late Professor J. S. Henslow, whose lectures on Botany at Cambridge as University Professor, I, as an undergraduate years ago, had the privilege of attending, was a sound, able, and very observant botanist. He was, moreover, well aware of the dimorphic condition of the primrose and cowslip (Darwin's "Life," viii., p. 297). In Huxley's "Life," he is described as "a botanist of the first rank," and Huxley further says of him, "a man with great acquirements and that calm, catholic judgment and sense which always seemed to me more prominent in him than in any man I ever knew" (vol. i. p. 226).[1]

Instead of such predecessors of Darwin being so contemptuously impugned for overlooking "so conspicuous and beautiful a contrivance for effecting cross-fertilization in the primrose"—as the primrose was supposed by Darwin to present—they are rather to be commended for strictly subordinating theory to natural facts. They thus happily avoided the error into which Darwin, in this instance at least, most assuredly and most conspicuously fell. Every

[1] We may be permitted to continue the quotation above from Huxley, in reference to Professor Henslow, one which all who knew him will endorse: "A man extraordinarily beloved by all who knew him." Sir Joseph Hooker married the professor's daughter.

observer, whether botanist or not, will, we feel assured, after careful observation of the case, attribute even to the bee itself—on whom the responsibility for any cross-fertilization would chiefly rest—those very sentiments with regard to the primrose that Wordsworth in the above lines attributes to *Peter Bell*.

We consider that it was most unfortunate for Natural Science that Darwin relied almost so exclusively on artificial observation, or, in other terms, on experiment, for the investigation and interpretation of natural laws in facts connected with the fertilization of flowers. The essential organs of reproduction in flowers are in the majority of cases so exceedingly sensitive that the results of artificial experiments with them sometimes reverse, and oftentimes obliterate, their natural fertility. Nature in this field is too sensitive for artificial experiment. Darwin, in our opinion, was led by his method to a very exaggerated view of the influence of cross-fertilization in the floral world. We shall endeavour in the following pages to offer some *pièces justificatives* of our opinion, founded, not on artificial observation, but on direct observation in the fields.

Explanation of technical terms are given, or referred to, in the Index.

We have carefully given the references to all the passages quoted, or referred to, in the following pages.

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THE PRIMROSE AND DARWINISM

CHAPTER I

THE PRIMROSE AND COWSLIP

Perhaps some of the most elaborate experiments of Darwin in reference to the cross-fertilization of flowers are to be found in connection with the *Order of the Primulaceæ*, as given in his book, *The Different Forms of Flowers on Plants of the Same Species.* This Order contains the common and well-known flowers—the Primroses and Cowslips. To these flowers, and to their Order, we shall primarily, though by no means entirely, confine our remarks. If the results of Darwin's experiments in regard to the primrose and cowslip are found unsatisfactory and untrustworthy, the result cannot but materially affect also, initially, and irrespective of ulterior considerations, the scientific value of Darwin's other experiments, conducted exactly on the same system, in the cases of all the other heterostyled dimorphic and trimorphic plants.

We may here explain one or two terms to the more general reader — technical terms — which cannot well be completely avoided in such a subject, and which, by such preliminary explanation, will render the treatment of the subject clear.

The word "heterostyled," which will be met with in the following pages, means that flowers of one and the same species, as the common primrose and cowslip, have each their styles of different lengths in different flowers. These different forms grow on different roots. Such flowers are also called dimorphic — of two forms — as having flowers differing in the relative position of their stigmas and anthers. When there are three different lengths of styles and stamens, in different flowers of the same species, such plants are said to be trimorphic, or of

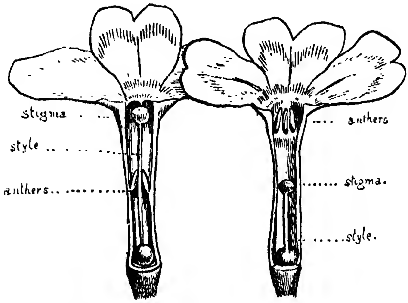

Fig. 1.
Long-styled form of primrose. Short-styled form of primrose.

three forms. The flowers generally of the primrose tribe (*primulaceæ*) are heterostyled and dimorphic. Some species are homostyled, a term used to denote that they exist only under a single form. This heterostylism is shown in the accompanying diagram (Fig. 1).

There are few observers of flowers but know that there are two different forms in the primrose. Some of the flowers have their stigmas—which are the termination of the styles—at the mouth of the corolla tube. These are commonly called "pin-eyed"; their anthers are midway down the tube. These are the long-styled flowers. Others,

on the other hand, have their anthers at the mouth of the corolla tube and their stigmas halfway down the tube. These are commonly called "thrum-eyed." These are the short-styled flowers.[1]

A few wild or garden primroses, or primulas, or polyanthuses, will immediately illustrate the difference between the two forms. Thus the chief difference between the two forms of flowers lies in the different lengths of their styles and stamens, and in the interchange of the relative position in these flowers of their stigmas and anthers (Fig. 1). These two different kinds are found on different plants growing side by side with each other, and both forms are equally common. It is exactly the same with the cowslip, and generally with the Primulaceæ, as our common garden Auriculas.[2]

[1] This term, "thrum," according to Johnson's Dictionary, was given to the end of weavers' threads, to which the anthers in the mouth of the corolla of the short-styled primrose or cowslip bore a considerable resemblance. Hence such short-styled primroses and cowslips were called "thrum-eyed."

[2] The common cultivated primulas and polyanthuses of our gardens exhibit, as we have said, the same different forms as to the position of anthers and stigmas as the wild primroses and cowslips, and can be obtained and observed during several months of the year. Many florists and others interested in gardening despise and reject the "pin-eyed" form of these flowers, as they consider the "thrum-eyed" so much the prettier, the stigmas of the pin-eyed breaking the breadth of colour in the corolla. Consequently, in many gardens the pin-eyed primulas are found to be much less numerous than the "thrum-eyed."

CHAPTER II

SUPERIOR NATURAL PRODUCTIVENESS OF THE SHORT-STYLED FORM OF COWSLIP AND PRIMROSE OVER THE LONG-STYLED FORM

DARWIN found, when these two different forms grew together in fields and woods, that those flowers which had short styles — styles ending with their stigmas halfway down the corolla — were much more productive as to weight, or number of their seeds, than those which had long styles. He marked, as they grew wild in spring, an equal number of each kind of flower of the cowslip and primrose, and gathered those marked ones when fully ripe in the autumn.

We first give the following summary as to the weight of seeds in the two different forms of the wild cowslip, the short-styled and the long-styled, as taken from Darwin's *Forms of Flowers*. In this table are compared the weight of seeds from an equal number of plants, an equal number of umbels, and an equal number of capsules of the two forms (Table 2, p. 19):—

	Number of plants.	Weight of seed in grains.	Number of umbels.	Weight of seed in grains.	Number of capsules.	Weight of seed in grains.
Short-styled cowslip .	10	92	100	251	100	41
Long-styled cowslip .	10	70	100	178	100	34

A similar experiment was repeated, the following year, in 1861. The wild plants were transplanted in the autumn into his own garden, into good soil, and all were treated alike. The result in the weight of the seeds of the two kinds was the following (" F. Fl.," Table 4, p. 20):—

	Number of plants.	Weight of seed in grains.	Number of umbels.	Weight of seed in grains.
Short-styled cowslip . .	100	1585	100	430
Long-styled cowslip . .	100	1093	100	332

" In all these standards of comparison," Darwin says, " it is evident that the flowers containing the short styles " (growing naturally) " were the most productive. In the first, in the ratio of nearly 4 to 3. In the last case, where the plants were placed in better soil, and not in a shady wood or struggling with other plants in the open field, the actual produce of the seeds was considerably larger. Nevertheless, there was the same relative result in favour of the short-styled plants (taking the fairest test, that of the umbels) as in the former case, nearly as 4 to 3 " (" F. Fl.," p. 20).

" Looking to these trials," Darwin says, " made during two successive years, on a large number of plants, we may safely conclude that the short-styled form is more productive than the long-styled form " (" F. Fl.," p. 20).

The superiority of the short-styled primrose over the long-styled plant in the matter of seeds was even more marked in the primrose than it was in the cowslip. " Nine long-styled and eight short-styled plants, growing together in the state of nature, were marked, and their capsules collected after being naturally fertilized, and the seeds from

the short-styled weighed exactly twice as much as those from an equal number of long-styled plants. So that the primrose resembles the cowslip in the short-styled plants being the more productive of the two forms" ("F. Fl.," p. 36).

CHAPTER III

ATMOSPHERIC INFLUENCES MINIMIZED IN DARWIN'S NET EXPERIMENTS

Now, to carry out his experiments as to cross- and self-fertilization of these flowers,[1] Darwin was obliged, in order to prevent bees or other insects from carrying pollen from flower to flower, to cover the plants with a fine, close-meshed net, "so that no insect but a Thrips" (which is a very minute insect, so minute that the shank of the thinnest pin is thick in comparison to it, and so small that it is scarcely much more than noticeable to the naked eye) "could pass through the net" ("F. Fl.," p. 24).

"In 1860," Darwin says, "a few umbels on some plants of both the long-styled and short-styled form of cowslip, which had been covered by a net, did not produce any seed, though other umbels on the same plants, *artificially fertilized*, produced an abundance of seed, and the fact shows that the mere covering of the net was not injurious" ("F. Fl.," p. 21. The italics are ours).[2]

[1] Self-fertilization means that the pollen of its own flower (or of a flower on the same root) fertilizes its own stigma. Cross-fertilization, on the other hand, means that pollen from a flower growing on a different root (in case of heterostyled plants, one of a different form) was applied to the stigma. In the case of self-fertilization, it is usually mentioned whether the pollen is of the same flower as the stigma, or from a different flower on the same root.

[2] Darwin's method of experimenting with the net is given on pp. 10, 11, in "Cross- and Self-Fertilization of Plants," and will be quoted in full below (Chap. XI.). There we shall see that Darwin, for cross-fertilization, used pollen grown outside the net.

Now, how Darwin could come to such a conclusion with the fact before him that the few umbels, which were not artificially fertilized with pollen naturally grown outside the net, produced no seed whatever, very much surprises us. On the contrary, we are very decidedly of opinion that the covering of a very close-meshed net was, for the following reasons, most injurious to all, but especially, as we shall see below, to the self-fertilized flowers.

1. The influence of the solar rays would be greatly diminished in passing through a close-meshed net, and consequently, they would be much debarred from exercising their full maturing power on the anthers, and so on the pollen of the *self-fertilized* flowers.

2. Radiation would likewise be almost entirely prevented by the net, and the dew would consequently fail to fall on the anthers.[1] The importance of this influence cannot be over-estimated. In the mornings of early spring, after clear and still nights, we have frequently found the flowers of the primrose bedrenched with dew. Occasionally the dew deposited on the anthers of the short-styled form has been so great as to lie upon the anthers, and entirely to fill the orifice of the corolla. Thus, the anthers of neither form could attain under such conditions their natural condition for fertilization. The stigmas would likewise be similarly affected, as the cups of their flowers were likewise very frequently filled with dew.

3. In calm weather, the covering of a close-meshed net would prevent the free access of the wind, and would prevent it from shaking, and so from freely disturbing and distributing the pollen. So close were the meshes of

[1] This test may be very easily made by placing a similar fine, close-meshed net on any short cut grass or lawn, and raised a foot or so above it, and removing the net in the morning before the sun is on the grass. After a clear and calm night in spring or summer, the grass outside the net will be covered with dew, whilst that under the net will be almost entirely dewless.

the net, in order to exclude all insects except the tiny *Thrips*, that Darwin tells us that in his experiments with *Linum perenne*, it required the wind to be high to pass through the net. His words are, "They were covered with a rather coarse net, *through which the wind, when high, passed*" ("F. Fl.," p. 93. The italics are ours). In that experiment there were a hundred meshes to the square inch. In the experiments with the primrose and cowslip, the meshes were equally close. In another place Darwin tells us, "In all cases the flowers were protected from the wind" (*Cross- and Self-Fertilization of Plants*, p. 23).

Moreover, Darwin tells us that one of the chief causes of the sterility or fertility of the plants which he experimented upon was "the absence or presence of the proper means by which pollen is applied to the stigma" ("Cr. and S. F.," p. 357). "Fertility," as Darwin tells us on several occasions, "is a very variable element with most plants, being determined by the conditions to which they are subjected" ("F. Fl.," p. 40). And again, "There is hardly anything more wonderful in nature than the sensitiveness of the reproductive elements to external influences" ("Cr. and S. F.," p. 472).

The minimizing of such natural atmospheric influences as those mentioned in this chapter was quite sufficient, in many cases partially, and in some cases completely, to sterilize the flowers. Such sterilization was only overcome in many instances by *applying artificially, pollen naturally grown*. Thus, in the experiment of 1860 (mentioned at the beginning of the chapter) "those flowers to which it was applied produced abundance of seed" ("F. Fl.," p. 20). The rest were unproductive.[1]

[1] The pollen from outside was usually, in his experiments, directly applied by Darwin to the flowers within the net. Darwin considers an experiment of his in which the flowers outside were only dragged over the heads of the flowers within an imperfect experiment. "In this case the flowers," Darwin says, "were legitimately but not fully fertilized" ("F. Fl.," p. 111).

CHAPTER IV

STERILIZING INFLUENCE PRODUCED BY DARWIN'S NET

We shall here produce only seven examples of the injurious effect of thus minimizing atmospheric influences in Darwin's experiments. These will amply suffice, though very many similar instances could be quoted, and a few more will occur in the course of these pages, to illustrate the injurious influence of the net upon fertilization. The effect of such minimizing is manifested sometimes in one aspect, sometimes in another. Sometimes immaturity of the pollen is met with from deficiency of the solar rays; in other cases the pollen is defectively disturbed and distributed by the flowers "being protected from the wind"; in other instances, the pollen tubes fail to reach the ovules from loss of the stimulus of the solar rays. The effect of minimizing the other atmospheric influences are almost necessarily in very many instances too subtle to be traced. We have already quoted Darwin's words as to the "wonderful sensitiveness" of flowers "to external influences."

The seven cases which we here produce will be those of *Salvia tenori;* the common broom (*Sarothamnus scoparius*); the cut-leaved mignonette (*Reseda lutea*); the red or purple clover (*Trifolium pratense*); the common yellow toad-flax (*Linaria vulgaris*); *Primula scotica;* and umbels of cowslips.

SALVIA TENORI.

Salvia tenori under the net, Darwin tells us, "was quite sterile; but two or three flowers on the summit of the spikes, *which touched the net when the wind blew*, produced a few seeds" ("Cr. and S. F.," p. 362. The italics are ours). Darwin continues, "This sterility was not due to the injurious effects of the net, as some flowers which I *fertilized* with pollen from an adjoining plant[1] produced fine seeds; and a small branch, when the net was removed, did the same when visited by bees." But these very facts prove distinctly, in our opinion, the sterilizing influence of the net. Whilst the flowers were under the net, and no artificial means applied, all the flowers were sterile except the few "which touched the net when the wind blew." Of the rest, some produced "fine seeds" when *artificially* fertilized. In these the artificial application of pollen supplied the place of the wind in its shaking and applying the pollen. This shaking would be more necessary in *Salvia*, as it is a genus of flowers which has only two anthers; the others were productive when he "removed the net." Of these latter Darwin says, "these were visited by bees and yielded seeds." But to attribute the capacity for fertilization in these flowers to the bees is perfectly gratuitous, as the flowers under the net (when bees were excluded), "when they touched the net and the wind blew," produced seeds without any cross-fertilization. A larger result, bees or no bees, would naturally follow from freer exposure to the wind, sun, and atmosphere.

[1] This pollen was doubtlessly from a flower grown outside the net according to Darwin's custom, as shown below in Chap. XI.

Common Broom (*Sarothamnus scoparius*).

Darwin says of the Common Broom (*Sarothamnus scoparius*), when under the net and bees excluded, that it is "*extremely sterile when not disturbed by being beaten by the wind against the surrounding net*" ("Cr. and S. F.," p. 360. The italics are ours). The exclusion of the full influence of the wind, the importance of which in the economy of these flowers their slender pedicels indicate, and the minimizing of the rays of the sun upon the pollen whilst still in the keel, sufficiently accounts for the extreme sterility which Darwin met with in his experiments with them. Those flowers only which were near the surface of the net, and so came in contact with it when beaten by the wind, produced seed. The rest were *extremely sterile.* Darwin truly remarks, in another allusion to this flower, "Plants thus protected from wind and insects" (and he might have added from the sun) "yield very few pods in comparison with those produced by neighbouring uncovered bushes, and sometimes none at all" ("Cr. and S. F.," p. 164).[1]

Cut-leaved Mignonette (*Reseda lutea*).

A very similar instance to the two preceding flowers is met with also in the Cut-leaved Mignonette (*Reseda lutea*). Two plants were taken by Darwin, and were protected under separate nets. "One of these," Darwin says, "became covered with spontaneously self-fertilized capsules as

[1] We only mention this case here incidentally. To this flower and to the order of Leguminosæ we shall allude more particularly in a future chapter (Chap. XIX.), as it is an order in which the agency of the wind is particularly important. The pollen is shed in these flowers at a very early stage, and lies in the keel, but needs generally the shaking of the wind to bring it on to the stigma.

numerous as those on the surrounding unprotected plants; so that it was evidently quite self-fertile. The other plant was partially self-sterile, producing very few capsules. When, however, this plant had grown tall, the uppermost branches became pressed against the net and grew crooked, and in this position the bees were able to suck the flowers through the meshes, and brought pollen to them from the neighbouring plants. These branches then became loaded with capsules; the other and lower branches remaining almost bare" ("Cr. and S. F.," p. 340).

Darwin here attributes the fertilization of the flowers which came in contact with, or in contiguity to, the net, to the bees. The spikes of the Cut-leaved Mignonette (*R. lutea*) are exactly similar in shape to the spikes of the well-known Sweet-scented Mignonette (*R. odorata*). The flowers of the latter plant, as every one knows who is acquainted with it, grow all round the spike. It is the same with *lutea*. The bees could not possibly reach with their proboscis the side or inside flowers, yet "the branches were loaded with capsules." Even the flowers that were pressed against the net the bees would only touch with their proboscis. All other contact the close-meshed net would debar them from. The proboscis or tongue of the bee would scarcely have on it a grain of pollen to convey from flower to flower, even in the case of those flowers which were pressed against the net, as when the tongue of a bee is withdrawn into its sheath it is cleaned of pollen. Nor is the *lutea* sweet-scented as the garden mignonette (*odorata*), and so it is comparatively sparsely visited. In our opinion, the fertility of these uppermost branches was entirely due to the sun's rays fully maturing the pollen and the stigma of those flowers which were contiguous to the net, and to the wind shaking the spikes which touched the net, so as to shake the pollen on to the stigma; "the other and lower branches remaining bare" because they were shut

out from such influences of sun and wind. Darwin was unfortunately blind to the sterilizing influences of his net. There was a difference between the two plants in their lower branches, but many accidental circumstances might have brought that about. The side and inside flowers of the spike show that the plant was not in its constitution sterile.[1]

Red or Purple Clover (*Trifolium pratense*).

"One hundred flower heads of the Red Clover (*Trifolium pratense*)," Darwin says, "on plants protected by a net did not produce a single seed, whilst 100 heads on plants growing outside the net, which were visited by bees, yielded 68 grains' weight of seed; and as 80 seeds weighed 2 grains, the 100 heads must have yielded 2720 seeds. I have often watched this plant, and have never seen hive-bees sucking the flowers except through holes bitten by the humble-bees. It is at least certain that humble-bees are the chief fertilizers of the common red clover" ("Cr. and S. F.," p. 361). Yet, in contrast to this last sentence, Darwin was fully aware how little humble-bees—on account of the length of the tube of the corolla—contribute to the fertilization of the red clover. Some pages further on, in the same volume, Darwin says, "I have already alluded to bees biting holes in the flowers for the sake of obtaining the nectar. In plants where the nectar is *thus stolen from the outside, there can be no cross-fertilization*. I have seen whole fields of red clover (*Trifolium pratense*) which had *every flower perforated*" ("Cr. and S. F.," pp. 428, 429. The italics are ours). Our own observation as to

[1] Very many similar instances to these three, as it occurs in *Lythrum salicaria* also ("F. Fl.," p. 148), would doubtlessly have occurred had similar possibilities been presented; but Darwin, when describing his method, says "the plants were placed under a net stretched on a frame and large enough to cover the plants without touching it" ("Cr. and S. F.," p. 10).

the boring of the florets of the clover is very similar to that of Darwin's. The great majority of the florets in the autumn crops of clover, when the weather is propitious and when the flowers are sufficiently advanced, we have found to be bored. Similar, or closely similar treatment, we may conclude, would necessarily be applied to the 100 heads of red clover growing outside the net which "were visited by bees"[1] ("Cr. and S. F.," p. 361), and which were sufficiently numerous and conspicuous to attract their notice.

Hence, in Darwin's experiments above, we have 100 heads of flowers, generally outside the influence of bees for fertilization—as the stigma and pollen are at the summit of the florets, and so are untouched when the florets are bored at the bottom by the humble-bees—but fully exposed to sun, dew, and wind, and all other natural atmospheric influences, producing 2720 seeds, whilst 100 heads of the same flowers under the net produce not a single seed.[2]

[1] The tube of the corolla of *Trifolium pratense* averages from 9 to 12 millimetres in length (25 millimetres being the equivalent of an inch). The tongue of a worker humble-bee "averages from 7 to 9, or, at most, 10 millimetres" (Lubbock, "Flowers and Insects," p. 61). After the middle of June, the chief foraging for the nest is done by the workers. "The female humble-bee soon remains at home altogether, leaving further out-of-door labour to the workers" (Saunders, "Hymenoptera Aculeata," p. 360). Hive-bees are necessarily excluded from obtaining the nectar by the shortness of their tongue, which is at most 6 millimetres in length. All other short-tongued bees are likewise excluded, by their having still shorter tongues than the hive-bee, from reaching the nectar of that flower: their proboscis averages only from $2\frac{1}{2}$ to 3 millimetres.

[2] Mr. Meehan, in America, with a net made of wire, met with a very different result from that found by Darwin. "Some years ago," Mr. Meehan says, "I covered patches of clover blossoms with wire netting to exclude the bees, yet all, every flower, I believe, perfected its seeds. Dr. Story Hunt, ex-president of the American Association for the Advancement of Science, and we together uncovered one patch, and examined a few mature heads, with the result as above stated" (*Nature*, vol. viii. p. 334).

That such complete sterilization was due to the presence of the net can scarcely be a matter of doubt.

When the red clover is growing in the fields, the pollen is ripe and begins to shed itself even before the flower itself is fully grown, and before it opens. At the same time, the stigma is likewise developed, and *remains in the keel* in very close contact with the anthers and their pollen. These arrangements are surely an indication that Nature has made provision for the fertilization of the flowers perfectly irrespective of the visits of bees. In inclement weather, when the red clover sets but little seed, this is consequently not to be attributed to the absence of bees, as some have assumed, for as we have seen above in the majority of the flowers of the clover crops, when the weather is propitious, the bees bore the corolla tubes. The failure of the clover to produce seed in such seasons is due to the inclemency of the weather alone.

Darwin tells us, in his "Origin of Species," that the fertility of this clover "absolutely depends on bees visiting the flowers" (p. 70). In another passage he says, "We may infer it is highly probable that if the whole genus of humble-bees became extinct in England, the heartsease and red clover would become very rare, or wholly disappear" (p. 53). In "Cross- and Self-Fertilization of Plants," Darwin says, "*Trifolium pratense* will more or less fail to produce seeds if the bees confine their visits to the perforations" (p. 425). Such statements are absolutely contradicted by the natural facts connected with the red clover and by the natural results as seen in Australia and New Zealand.

Mr. Syme, in his book on the "Modification of Organisms," makes the following statement: "Darwin says that *Trifolium pratense* will not produce seeds unless it is visited by humble-bees. The statement has been accepted without question, and some settlers in New Zealand have imported

humble-bees into that colony in order to secure seed from the flowers, which bloom freely enough, but were believed, on Darwin's authority, to be infertile. But this is quite a mistake. Red clover seed had been grown and exported from New Zealand long before the humble-bee was introduced there; and I am informed by one of the leading Melbourne seedsmen that he has been supplied with this seed, grown in the western district of Victoria, for the last seventeen years, although no humble-bees have ever been introduced into that colony" (p. 112).

If Darwin's idea were correct, the farmers in England would have a very sorry time indeed as to crops of clover seed. In inclement seasons the flowers naturally fail to produce much sound seed, and in propitious seasons Darwin had seen "whole fields of red clover which had every flower perforated." Thus bad seasons, and propitious seasons, would be equally fatal to the farmer's chance of obtaining good clover seed. But, happily, the farmer "takes no 'count of the bees." He never examines whether the florets are bored. If the weather has been hot and dry, he knows that the seed will be good and the crop very productive; yet these are the very seasons in which the humble-bees are the most numerous and the most active in boring the corollas.[1] The very fact of abundant crops of sound clover seed in such seasons is of itself a sufficient witness against Darwin's idea, and a strong witness also as to the sterilizing influence of Darwin's net.

Though the crop is precarious, a circumstance which arises almost solely from the precariousness of the weather, there is no danger as to the red clover "wholly disappearing," even if the humble-bees do not give up their bad

[1] The late Mr. Fred Smith, of the British Museum, says, "The number in the surface-building humble-bees are greatly increased or diminished by the state of the weather; in fine, dry seasons nests have double the number of inhabitants to what are found in them in wet and unfavourable ones" ("Brit. Hymen. Acul.," p. 197, pt. i.).

habits of "stealing the nectar, and confine their visits to the perforations," nor would there be any danger even if "the whole genus of humble-bees became extinct in England." It is always the second crop—not the first, or, as the farmer calls it, the maiden crop—from which the farmer obtains the seed. If it has been unpropitious weather, the farmer feeds off the crop with sheep, or ploughs it in. He knows that it will not in such a case pay him to thresh and operate upon the seed for its cleaning. He could not sell it if bad, as bad seed and good seed can be readily told by the colour. If good, the seed is purple; if bad, yellow or whitish, or of a wizened brownish appearance. The value of the crop depends upon the percentage of good seed, as even in the finest seasons some small percentage of bad seed is always present.

We were told by one farmer that he made on one occasion, when the summer had been hot and dry, £180 from a crop of ten acres of clover seed. Another farmer told us that after a similar season he cleared £150 from six acres. As each floret in a head of clover only produces a single seed, there could have been no failure in productiveness, or in the quality of the seed, by the boring of the florets by the humble-bees. The farmer's experience with respect to the red clover utterly contradicts Darwin's theory that "*Trifolium pratense* will more or less completely fail to produce seeds if the bees confine their visits to the perforations." Their experience also contradicts his theory concerning seedlings raised from such seeds. "The perforated flowers of the species which are capable of fertilizing themselves, will yield only self-fertilized seeds, and the seedlings in consequence will be less vigorous" ("Cr. and S. F.," p. 438). If farmers had found by experience that seeds grown in such hot and dry seasons when the florets are most, and almost universally, bored, were of an

inferior quality, the prices mentioned above would never have been obtained.[1]

LINARIA VULGARIS.

Of the Yellow Toadflax (*Linaria vulgaris*), the next instance which we cite, Darwin says, "Seeds were taken

[1] Darwin propounds a curious and very far-fetched theory about flowers which are subject to being perforated by humble-bees, and the consequent flux and reflux in numbers both of the flowers and of the bees. The grounds on which he builds his idea are, as far as the red clover is concerned, contrary to the facts connected with its seeds and its seedlings. "Humble bees are more inclined," he says, "to perforate flowers which grow in numbers near together than single flowers, as flowers growing together afford a rich booty, and are more conspicuous." This is doubtless the fact in a very considerable measure, as single heads of clover growing in pasture fields, being much less noticeable, are usually much less perforated, than those growing in clumps or crops. "All plants," Darwin continues, "must suffer in some degree when bees obtain their nectar in a felonious manner by biting holes in the corolla, and many species, it might be thought, would be exterminated. But here, as is so general throughout Nature, there is a tendency towards a restored equilibrium. If a plant suffers from being perforated, fewer individuals will be reared; and if its nectar is highly important to the bees, these in their turn will suffer and decrease in numbers; but, what is much more effective, as soon as the plant becomes somewhat rare, so as not to grow in crowded masses, the bees will no longer be stimulated to gnaw holes in the flowers, but will enter these in a legitimate manner. More seed will then be produced, and the seedlings being the product of cross-fertilization, will be vigorous, so that the species will tend to increase in number, to be again checked, as soon as the plant again grows in crowded masses" ("Cr. and S. F.," p. 438.)

But against this theory of flux and reflux in the flowers and humble-bees, stand the facts that there is no proof that the productiveness of the red clover is impaired by the bees obtaining the nectar "feloniously;" nor any that fewer individual flowers are reared from the seeds in consequence of such boring. There is consequently also no decrease of nectar, and no flux and reflux of bees; nor is there any proof that the seedlings arising from cross-fertilization are more vigorous than those which are ordinarily produced. Facts are against such a supposition.

from wild plants and sown in my garden. Five plants were covered with a net, the others being left exposed to bees, which incessantly visit the flowers of this species, and which, according to H. Müller, are the chief fertilizers. This excellent observer remarks that as the stigma lies between the anthers, and is mature at the same time with them, self-fertilization is possible. But so few seeds are produced by protected plants that the pollen and stigma of the same flower seem to have little power of mutual interaction. The exposed plants bore numerous capsules. Five were examined and contained each an average of 166 seeds. The finest capsules of the protected plants contained an average of 23 seeds. So that the average number of seeds in the capsules of the exposed plants to the average number in the finest capsules of the protected plants was as 100 to 14" ("Cr. and S. F.," p. 88).

Now, all who are acquainted with the flowers of the yellow toadflax know that it has a particularly long spur (considerably longer even than that of the tube of the red clover, *Trifolium pratense*), springing from the flower where the corolla is attached to the stem, and that at the lowest part of the spur the nectar lies. The length of the narrow spur alone, without taking any account of the mouth part of the corolla (which is about 3 millimetres in length), averages 14 to 16 millimetres, and in some flowers reaches to even 18 millimetres. In consequence of its length, the *worker* humble-bees are necessarily obliged, if they are to obtain the nectar, to bite through the spur towards its middle or lower end. No influence in such a case is exercised by them in effecting any cross-fertilization of the flowers, as the pollen and stigma are above the spur.

We gathered on one occasion in the first week of August—during which month and July, the flowers on the toadflax, and the humble-bees as well, are the most

abundant—a great number of flowers in a field where very many plants were growing. Amongst all these there were but two flowers in which the spur was not bitten through; in some cases it was even bitten through in two or three places, the tip of the spur hanging on by the merest shred.

In September, when its flowering season is drawing towards its close, and when humble-bees are becoming much scarcer and less vigorous, the majority of the flowers are not bitten through. It is markedly so after, and even before, the middle of the month. But at such a period very few humble-bees are seen to visit them at all. When the flowers are thus let alone, the nectar will rise in the spur three or four millimetres. Even with this reduction in length of the distance of the nectar[1] from the mouth of the corolla, it is beyond the reach of the ordinary worker humble-bees, which, almost alone, are upon the wing at that time. We have seen occasionally in the middle of September, small humble-bees fly to the flowers, and if the spurs were not bitten through, fly off at once to other species. Yet even these later flowers usually produce abundant seeds.

We wonder that Darwin did not notice this boring of the spur by the bees in the case of *Linaria vulgaris*. We can only account for it by its being the first of the flowers on which he experimented. Darwin says, too, that his experiment was not carried out in this case with such particular care as in his subsequent experiments. "The trial was afterwards repeated with more care, as this was the first of the plants experimented on" ("Cr. and S. F.," p. 88). Even the flowers of its cousin *Antirrhinum*—the common snap-dragon of our gardens—which is not spurred like *Linaria*, but has only a short projecting

[1] The nectar then can be easily seen, and measured, as the spur itself is transparent.

tube, scarcely more than 3 or 4 millimetres in length, are often all bitten through. In consequence of this biting through of the spur of the *Linaria*, the results of Darwin's experiments become in this case almost absolutely a comparison, not between crossed and uncrossed flowers, but between uncovered and covered ones; the result being, according to Darwin, as 100 to 14 in the number of seeds produced.[1]

[1] Without carefully watching the action of a bee when it visits not only these flowers but a few other flowers, which have monopetalous corollas, incorrect conclusions as to the method of the fertilization of such flowers may be drawn. Thus, *Erica tetralix* (the Cross-leaved Heath), the corolla tube of which is only 6 millimetres in length, and which, therefore, as far as mere length is concerned, is easily accessible to the humble-bee, is constantly, almost universally, in the height of the season, perforated by them. This boring of the corolla is due to the position and arrangement of the anthers. The anthers are arranged in a compact, broadish circle round the style just within the narrow mouth of the corolla. As the anthers fill out and ripen, they almost close up the direct passage to the nectar. This perforating is met with more universally in the latter part of July and in August. Even in the earliest appearing flowers it is met with, but is not so universally the case as later. Towards the middle and the end of July and August, the humble-bees are most numerous, and are to be met with in greater numbers amongst the heather, as honey-bearing flowers in the same districts are becoming scarcer. Darwin notices this difference, and observes in his later visit to the heather at Bournemouth, that "the extent to which humble-bees carry on the practice of biting holes is surprising. A remarkable case was observed by me at Bournemouth. I took a long walk, and when I had gathered a handful of the flowers of *Erica tetralix*, I examined them all under a lens. This I repeated many times, and though many handfuls were examined, I did not succeed in finding a single flower which had not been perforated" ("Cr. & S. F.," p. 429). The flowers are usually not perforated until they open. This flower is very seldom visited by the hive-bee unless thus perforated. Then we have seen it make use of the perforations. The beautiful *Erica ciliaris* (of the Dorset and Cornwall heaths) which has a longer corolla than *tetralix*, being 8 millimetres in length, is universally perforated. The *Erica cinerea* (the purple or Scotch Heath) has a shorter corolla, averaging only 4 millimetres in length, nor are the anthers so large as in *tetralix*.

But even if none of the spurs were bored, and the bees visited the *Linaria* properly at the mouth, still no valid conclusion could be drawn from such an experiment as to the superior effect of cross-fertilization in this case, as the *protected* flowers were deprived of the full influence of the solar rays for the maturing of the pistil and pollen, and of the wind, and of other atmospheric influences, which would be quite sufficient to cause in them an inferior fertility. This inferiority in fertility was produced by the sterilizing influence of the net.

PRIMULA SCOTICA.

The sterilizing effect of the net is seen remarkably in *Primula scotica.* This is a homostyled flower where the stamens and stigma are both at the mouth of the corolla. Darwin tells us that Mr. Scott, of Edinburgh, found that "the flowers yielded an abundance of seed when fertilized by their own pollen" ("F. Fl.," p. 50). In another place, Darwin says of it, "it is fertile with its own pollen, but is extremely sterile when insects are excluded" ("Cr. and S. F.," p. 362). Darwin would explain this by saying that "this depends merely on the coherent pollen not readily falling on the stigma without their aid." Yet Mr. Scott's experience, as recorded just above, was different. This sterility of this primula in Darwin's experiments was, in our opinion, undoubtedly attributable either to the immaturity of the pollen from being grown under the net and the coherency arising from this immaturity, or to the exclusion of the wind. Moreover, the pollen of this

It consequently does not present equal difficulties to the bee, and even the hive-bee can pass its proboscis between the bases of the adjoining anthers. Yet even this flower will be found occasionally perforated. When the pollen is ripe, the buffeting of the wind displaces the anthers, and so lets free the pollen. When the fruiting commences, the bees cease to visit these flowers.

primula is not more coherent than that of the primrose, which, as we shall see as we proceed, fertilizes itself without any visits from insects.

Umbels of Cowslips.

The last case which we shall mention here is that of the *Umbels of Cowslips.* In 1861, 24 umbels of short-styled cowslips, and 74 of long-styled ones, were similarly covered, "just before they expanded their flowers" ("F. Fl.," p. 21). The result of this experiment—and here there was no artificial fertilization introduced—was that the 24 umbels produced 1¼ grains' weight of seed, and the 74 long-styled umbels produced none at all. "Judging," Darwin says, "from the exposed plants which grew around in the same bed, the above 24 short-styled umbels should have produced 92 grains' weight of seed; and the 74 long-styled umbels ought to have produced 200 grains' weight of seed." Darwin accounts for the contrast between the produce of the flowers outside and of those under the net, by the presence of insects in the former case, and the absence of insects in the latter, and draws this conclusion "We see thus that the visits of insects are absolutely necessary to the fertilization of the cowslip" (*Primula veris*) ("F. Fl.," p. 22).[1]

But such an explanation, for the reasons given above and for others which will be adduced below (Chap. VII.) both from the cowslip and the primrose, proves in our opinion nothing of the kind; but on the contrary, that the presence of the net alone fully and adequately accounts for the non-fertilization of the flowers. Minimize the sun, the dew, the wind, and other atmospheric agencies, in such a

[1] These umbels will be further alluded to in Chapter VII.; in which chapter we shall see that the cowslip is very rarely indeed visited by bees.

way as practised in these experiments, and not all the insects in the world would have caused sound and full fertility.[1]

It is strange that, in the face of the examples which have been recorded in this chapter, and of others which will be recorded below, that Darwin should say, "Experience has proved to me that, independently of the exclusion of insects, the seed-bearing power of a plant is not lessened by covering it while in flower under a thin net supported on a frame" ("Cr. and S. F.," p. 357). This impression led Darwin into manifold erroneous conclusions.

[1] In reading Darwin's books, it is necessary to bear this fact constantly in mind, for the reader will be brought face to face with results from Darwin's net which it will be continually necessary heavily to discount. This is particularly noticeable in such chapters as Chap. IX., "Cr. and S. F.," where there is an excursus on "self-sterile" plants. Many of these plants are not English plants; many were kept in a hothouse, and expected to be fertile; if not, they are classed as "self-sterile." Sometimes both these circumstances—foreign plants and a hothouse in which the experiments are made—are combined. As instances of this last class, some species of *Oncidium* and of *Maxillaria*, cultivated in a hothouse in Edinburgh, "were quite sterile with their own pollen" ("Cr. and S. F.," p. 331). All of these cases, which are there classed as sterile, were either grown in a hothouse or under a net.

CHAPTER V

THE NATURAL PRODUCTIVENESS OF THE COWSLIP AND PRIMROSE *REVERSED* BY THE NET

Let us now turn to Darwin's experiments, where the two different forms of cowslips—the long-styled and the short-styled—are covered by the net, and where the two forms are subjected to exactly similar treatment of intercrossing. In one set of flowers, the long-styled stigmas are crossed with pollen from the short-styled ones, and the short-styled flowers are crossed with pollen from the long-styled.

The result is as follows :—Under the net, 100 capsules of

The long-styled cowslip,

crossed by pollen of the short-styled, produced 62 grains' weight of seed ; of

The short-styled cowslip,

crossed by pollen of the long-styled, produced 44 grains' weight.

Again, one set of flowers, the long-styled, are fertilized by their "own form" pollen, and the short-styled flowers are similarly fertilized by their "own form" pollen.[1]

This result follows :—Under the net, 100 capsules of

The long-styled cowslip,

fertilized by "own form" pollen, produced 42 grains' weight of seed ;

[1] The term "own form" pollen is used by Darwin to signify pollen taken not from its own flower, but from a flower with the same kind of style, growing on a different plant ("F. Fl.," 24).

The short-styled cowslip,

fertilized by "own form" pollen, produced 30 grains' weight.

By this we see that, in both the experiments above, the long-styled cowslips are the more fertile of the two, in the proportion of 3 to 2 and 4 to 3 ("F. Fl.," Table 6, p. 25).

Thus we see that, under Darwin's method of experimenting, the natural productiveness of the two sets of cowslips is *completely reversed.* When naturally grown, we have already seen from Darwin's tables that the short-styled were in productiveness to the long-styled as 4 to 3; but under the net the long-styled were superior to the short-styled, in the one case as 3 to 2, in the other as 4 to 3.

Let us now take, in the same way, the case of the primrose. The primrose, like the cowslip, has the two forms. Under the net, when the primrose was treated in exactly the same way as the cowslip above, it gave the following results as to the average number of seeds ("F. Fl.," Table 9, p. 37):—

The long-styled primrose,

crossed by pollen from short-styled, produced 66 seeds;

The short-styled primrose,

crossed by pollen from the long-styled, produced 65 seeds.

And again,

The long-styled primrose,

fertilized by "own form" pollen, produced 52 seeds;

The short-styled primrose,

fertilized by "own form" pollen, produced 18 seeds.

Now, we have already seen that when Darwin gathered capsules from primroses growing together in their natural habitats, he found that "the seeds from the short-styled weighed exactly *twice as much* as those from an equal

number of long-styled plants. So that the primrose resembles the cowslip in the short-styled form, being, when growing naturally, the more productive of the two forms" ("F. Fl.," p. 36).

But here, under the net, in the first case they are placed on an equality; in the second case, the long-styled is to the short-styled in fertility as 5 to 2; so that in both cases there is a *great reversion* under the net from what takes place under natural conditions.

Such a system of experiments as those above is evidently most untrustworthy as a scientific indicator of what takes place in those two flowers in a state of nature, for it actually reversed, in both crossed and uncrossed flowers, the productiveness found under nature in the case of both cowslips and primroses in weight and number of seeds.[1]

[1] The "summaries" in the tables which Darwin gives, when the two legitimate (or illegitimate) unions are jumbled up together, are very confusing and slightly deceptive.

Such summaries, as in Tables 6 or 9, or such Tables as 12 (p. 46), or 33 (p. 246), are consequently very valueless, as the short-styled primrose, as we shall see below, absolutely contradicts Darwin's conclusions, whilst there is no equally absolute contradiction afforded in the case of long-styled flowers. The two forms should not, therefore, be mixed together, as no trustworthy conclusion can be drawn from such summaries.

CHAPTER VI

IS CROSS- OR SELF-FERTILIZATION THE MOST PROBABLE WITH THE PRIMROSE?

Let us now consider whether cross-fertilization or self-fertilization is most probable when the primrose grows wild in its natural habitat and with its natural surroundings. Every botanist is well aware that the tube of the corolla of the primrose is of very considerable length. It requires consequently an insect with a long tongue or proboscis to reach the nectar at the bottom of the tube. Such insects are chiefly the humble-bees, moths, and butterflies.

Humble-bees are not in the habit of visiting the primroses. If such a case occurs, it is most exceptional. Darwin, speaking of his own experience, says, "The primrose is never visited—and I speak after many years of observation—by the larger humble-bees, and only rarely by the smaller kinds"[1] ("F. Fl.," p. 56).

[1] This rare visitation to the primrose by the "smaller kinds of humble-bees" (*i.e.* the worker humble-bees), spoken of by Darwin here, supposing even that they were upon the wing, could be very easily accounted for. The tube of the corolla of the primrose (and also of the cowslip) averages 12 to 14 millimetres in length. In fact, in favourable situations, the corolla tube of the primrose is very frequently 16 millimetres in length. The tongue of the smaller or worker humble-bees averages, as we have said above (Chap. IV.), 7 to 9 millimetres. The only smaller worker humble-bee, whose tongue even approaches in length that of the tube of the corolla,

In all our experience we have never seen a humble-bee, either of the larger or of the smaller kinds, visiting the flowers. Once we saw a smaller short-tongued bee, *Andrœna nigroœnea*, sitting on the petal of a primrose, but it was only sunning itself, as its proboscis was far too short to reach the nectar. Even if it had been there for gathering pollen from the short-styled flower, which it was not doing, it would have been no agent in cross-fertilization, as it would not visit the long-styled flower at all, since neither nectar nor pollen of such long-styled flower could be reached by its tongue. Four insects, and four insects only, with a long proboscis, and each on a *single occasion only*, have we seen visiting the primrose and probing for honey. One was the *Anthophora pilipes*, a comparatively quite rare insect, which flew from primrose to primrose, intercalating these visits with visits to the dog-violet (*Viola canina*). This was on the 27th of April, when the primrose season was more than half over. Another was a Diptera, the two-winged humble-bee fly (*Bombylius discolor*), also a comparatively rare insect. This instance, too, was when the season of primroses was well on, past the middle of April. The other two were butterflies—the brimstone butterfly (*Gonepteryx rhamni*) and the cabbage butterfly (*Pieris brassicæ*). These were on the 19th of April.

would be that of *Bombus hortorum*, whose tongue exceeds that of all the other humble-bees, and varies, according to the bee's size, from 8 to 11 millimetres. But, strangely, none of these smaller humble-bees, as a rule, appear until the wild primroses generally have been some little time out of flower. Possibly Darwin may have mistaken an *Anthophora* for a smaller humble-bee; the resemblance between the two is close, and the tongue of the Anthophora varies from 15 to 18 millimetres, or, as H. Müller gives it, 19 to 21 millimetres ("F. Fl.," p. 385). It is earlier out than the worker humble-bee, and it is also a comparatively rare species of bee. All other smaller kinds of bees, such as the hive-bee, whose tongue is only 6 millimetres long, and the *Andrenidæ* generally, whose tongues are still shorter than those of the hive-bee, are necessarily excluded.

Each of the four were, as we said above, limited to single instances. This was our experience, after seeing and examining thousands and thousands, we might say millions, of the flowers.[1]

Darwin, in his lack of evidence in respect to humble-bees visiting the primrose, was driven, in order to square Nature with his theory, to attribute the fertilization of the primroses to moths, and to say (after his statement quoted above about the "larger and smaller kinds of humble-bees"), "hence the fertilization of the primrose must depend almost exclusively upon moths" ("F. Fl.," p. 56); and, again, in another place, "I suppose, therefore, that the primroses are commonly fertilized by nocturnal Lepidoptera" ("F. Fl.," p. 36). But of this there is no evidence, nor does Darwin give any. On the contrary, no day-flying moths have been seen to visit the flowers. It is, therefore, an equal probability that they are unvisited by night-flying moths at night.[2]

[1] Mr. T. A. Briggs, who gives his observations in the neighbourhood of Plymouth as to the fertilization of the primrose, seems to have had almost an exactly similar experience to our own. He met with an *Anthophora*, a *Bombylius*, and a brimstone butterfly visiting the flowers. *Journal of Botany*, vol. viii., p. 190.

[2] Darwin, on several other occasions, makes use of the supposition or suspicion of nocturnal moths in order to dispose of the difficulty of the self-fertilization of flowers. A suspicion occurs in reference to *Linum catharticum*, which is with the greatest rarity visited by butterflies or moths by day. "H. Müller," Darwin says, "has only once seen the flowers thus visited during the day; but it may be suspected that they are visited during the night by small moths" ("F. Fl.," p. 101). H. Müller himself, however, disposes of such a supposition, as he tells us that the flowers of *L. catharticum* "close in the evening." The suspicion occurs again with reference to the Hop Trefoil (*Trifolium procumbens*) and the lesser Trefoil (*Trif. minus*). To this we shall allude further in Chap. XIX. The same suspicion is repeated in the case of *Fumaria officinalis* and *Fumaria capreolata*. Of the former Darwin says, "I have often watched the flowers, and so has Hildebrand, and we have never seen an insect visit the flowers." Yet Darwin suggests that "it may perhaps be "Cr. and S. F.," p. 147.

Darwin was inclined to attribute the absence of bees from the primroses either to the odour of the flowers or to the taste of their nectar ("F. Fl.," p. 56). If this were also the cause that neither butterflies nor day-flying moths visited the flowers, this would equally affect the night-flying moths as well. The odour which was disagreeable, or the nectar which was distasteful, to the one, would be equally so to the other; night or day would make no difference whatever in this respect. Without some enticement by night which the flowers do not possess by day, as is the case with the *night-scented* stock (Hesperis), but is not the case with the primrose, there is no ground for supposing that night-flying moths treat a flower by night differently from the way in which their congeners habitually treat it by day.

Moreover, in March and in the early days of April, when the early primroses are in bloom (usually preceding in this respect, by two or three weeks, the cowslips), bees, butterflies, and moths, are infinitely scarce, whilst the primroses, in many situations, are infinitely numerous. The clear nights of March and early April are also very frequently frosty and unfavourable for insects, even if they were existing in their imago stage, being upon the wing at night. But upon such insects—the moths—Darwin is obliged to rest his case of cross-fertilization being effected in the primrose by insects with a long proboscis.[1]

visited at night by small moths" ("Cr. and S. F.," p. 366). The same absence of insects occurred as to *F. capreolata* during the day, yet Darwin says, because some of the flowers were slightly open in the morning, that "it is clear that some of the flowers had been visited by insects" (p. 366). It is equally clear, in our opinion, that the wind might have affected the same. Even "small and inconspicuous flowers, which are never, or rarely visited by insects during the day" are yet suspected of being "occasionally visited and intercrossed by nocturnal insects" ("Cr. and S. F.," p. 441).

[1] The wild primrose is in bloom usually from the middle of March to the end of April. We are informed that very few night-moths

Yet, in spite of the negative relation in which insects are thus seen to stand to the primrose, even according to Darwin's own experience, Lord Avebury applies, to *primroses in particular*, Darwin's ingenious exposition of the supposed action of an insect with a long proboscis in effecting cross-fertilization which Darwin had applied to the cowslip ("F. Fl.," p. 23). "An insect thrusting its proboscis down a primrose," Lord Avebury says, "of the long-styled form, would dust its proboscis at a part which, when it visited a short-styled flower, would come just opposite to the head of the pistil, and could not fail to deposit some of the pollen on the stigma, and conversely, an insect visiting a short-styled plant, would dust its proboscis at a part further from the tip, which, when it subsequently visited a long-styled flower, would again come just opposite to the head of the pistil. Hence we see, by this beautiful arrangement, insects must carry the pollen of the long-styled form to the short-styled, and *vice versa*."[1] Mr. Wallace repeats the same exposition of the action "of bees and moths visiting the flowers of the cowslip," and then adds, "the same thing was found to occur in the primrose." "Nat. Select. p. 465

Now, "this beautiful arrangement," in Lord Avebury's idea, whereby insects "must effect" cross-fertilization in the primrose, cannot be true in any way in the case of the

(*Noctuadæ*), excepting members of the *Tæniocampa* and a few of the *Geometridæ*, appear before May, and even few in that month, June being the first month in which they begin generally to appear; that there are eleven English species of the *Tæniocampa*, and that these feed especially on the spring sallows. H. Müller, whose "Fertilization of Flowers" is written especially in behalf of cross-fertilization, omits all reference to insect visits to the primrose, as to the cowslip also. This shows that he had no evidence in its support. He merely refers (p. 383) to Darwin's paper, "On the Two Forms or Dimorphic Condition of Primula."

[1] Sir John Lubbock (now Lord Avebury), "British Wild Flowers in Relation to Insects," p. 39.

primrose, as, unfortunately for such a theory, neither bees, nor butterflies, nor any insects with a proboscis long enough to reach the nectar, are accustomed, as we have seen, to visit the primrose.

We are thus driven, in the case of the primroses, to smaller insects, to insects which must pass up and down the corolla, such as *Thrips*, for their supposed cross-fertilization. But even of insects generally Darwin says, "It is surprising how rarely insects can be seen, during the day, visiting the flowers" ("F. Fl.," p. 36). With this observation every one who has at all carefully noticed and examined the primrose flowers will agree. It is not only rare, as Darwin says, but it is a *remarkable exception* to see any insect, except a *Thrips*, present on a primrose. During one year we gathered over two thousand primroses from more than two thousand different roots and in different situations, as woods, open hedgerows, and roadsides, from March 17th to considerably past the middle of April, which we opened and examined, and we found, besides the *Thrips*, only one small beetle and one beetle caterpillar. But, besides these primroses, we observed thousands upon thousands of ungathered primroses, and yet that was all the living insect life, except the one short-tongued bee (*Andrena*), the *Anthophora*, the *one Bombylius*, and the *two butterflies*, found or seen upon them. Cross-fertilization could not in any way, therefore, be effected by insects in the primrose.

Moreover, the *Thrips*[1] is so minute an insect that the pollen of a single flower, on which, as far as we have been able to observe, it chiefly feeds, would amply supply the

[1] These insects of the Thrips species vary in colour in the different flowers, but they can easily be recognized under a pocket-magnifier by their wings, as the edges of their wings are, almost universally, furnished with an exceedingly delicate fringe of fine hairs, which most frequently extends round their whole margin.

wants of many of these insects. Darwin allows that even the amount of pollen which the Thrips would convey from plant to plant could have very little influence in causing any effectual cross-fertilization of the stigmas. "A cross of this kind" (from a *Thrips*) "does not produce," Darwin says, "any effect, or, at most, only a slight one" ("Cr. and S. F.," p. 22). The chief influence which it might exercise would necessarily arise from its feeding on the pollen, and so disturbing and causing it to fall on the short-styled stigma, or from its conveying the pollen of both forms of flower down which or up which it passed, to each flower's own stigma, and so would contribute to the self-fertilization of that flower. Darwin allows the fact of such insects causing the self-fertilization of these flowers. "Minute insects such as Thrips, which sometimes haunt the flowers," Darwin says, "would be apt to cause the self-fertilization of both forms; and this self-fertilization would be much more apt to occur when it was visiting the short-styled form" ("F. Fl.," p. 23).

Darwin, when speaking, not of the primrose, but of flowers generally, says that he has "more than once seen a minute *Thrips*, with pollen adhering to its body, fly from one flower to another flower of the same kind" ("Cr. and S. F.," p. 420). We are not astonished at the rarity of the occasions that his words "more than once" indicate, on which he witnessed the *Thrips* in flight. Yet, in his examination of the flowers of the primrose, he must have seen and disturbed hundreds of these tiny insects. We have never seen it fly. We have repeatedly tried it on the palms of our hands in the fields and woods, and have brought it back from the woods with us, and have provoked it to fly with a piece of grass or primrose stem, but have never succeeded in making it fly on any single occasion. It would give a very minute leap, usually from a quarter of an inch to an inch in length. This seems to be, as far as

our experience goes, its usual habit. This habit would necessarily confine it, as a rule, to a single root, and so to a single form of the primrose. It would debar it, except on rarest occasions, from being an agent in cross-fertilization.[1]

In the short-styled form, the anthers—as the flower-stalk is, when in flower, naturally erect—are placed just above the stigmas, and when the flowers are shaken by the wind, or disturbed by an insect, as the *Thrips*, passing down the flower, or more particularly when the *Thrips* is feeding on the pollen above—for they are found, when the flower is gathered, chiefly among the stamens—some portion of the pollen would be dislodged, and would drop upon the stigmas below. "These stigmas are eminently liable," Darwin says, "to receive their own pollen, for when I inserted a bristle or other such object in the corolla of this form, some pollen was almost invariably carried down and left on the stigma" ("F. Fl.," p. 23).

In examining very considerably over five hundred stigmas of each kind, both of the long- and of the short-styled forms, we found, as a rule, the pollen in the short-styled deposited on the top and upper half of the stigma; on the other hand, in the long-styled form, the pollen was in most cases, when the pollen was mature, deposited on the bottom and lower half of the stigma. So much so was this the case that we could almost without fail, when the pollen was shed, decide by the position alone of the deposited

[1] Mr. Dallas, in his "Elements of Entomology," notices this characteristic of Thrips. He says, "All these insects (Thrips) are also remarkable for their possession of the power of executing leaps of considerable extent in comparison with their size, by the agency of their abdomen, which they bend under them and suddenly extend" (p. 182). On one occasion we had an accidental instance of its reluctance to use its wings for flight. We had brought one home to test it. We were touching it with a primrose stalk when close to the edge of the writing-table. In its short leaps it leapt over the edge of the table; but, instead of flying, it fell to the ground, landing close to the table's foot, directly under the edge of the table.

pollen to which form the stigma belonged. Such distinctive difference generally in the position of the pollen on their respective stigmas would not have been seen if it had been deposited by insects.[1]

Moreover, the anthers in both forms, but more particularly so in the short-styled form, as in the long-styled they are pierced and kept very slightly apart by the style passing through them, curve inwardly at the top toward the centre of the corolla tube, and with their triangular apices they form in the short-styled, when the pollen is ripe, in nearly every case, an almost perfectly closed roof over the tube of the corolla below, so that the corolla is almost a closed box, with its contained stigma within. This is a most noticeable feature in the short-styled primrose when the pollen is mature. It would consequently be most exceptional for any foreign pollen to pass from the outside into the corolla of the short-styled. The anthers open on their inner and under surface into the corolla tube, and into it discharge their pollen.

If there were any validity in the idea so strongly pressed by Lord Avebury—and especially applied to the case of the primrose ("Flowers and Insects," pp. 28, 36–38, *Popul. Natur. History*, p. 122)—that Nature has in many cases made arrangements "that self-fertilization should be prevented," such an idea in this case is singularly inapplicable.[2]

Nature, indeed, would seem to be acting in wanton waywardness to trap the corolla tube with a close covering of anthers, with their hard backs facing outside; to place these anthers directly overhanging the stigma; to arrange that the anthers should burst inwardly; and yet that, with

[1] In making such examination, care must be taken in removing the corolla of the short-styled flower, and in opening the corolla of the long-styled one, that no pollen falls upon the stigma.

[2] Darwin says that such a view is a "tempting view" in reference "to several species of primula, yet from facts with reference to other species this view can hardly be admitted" ("F. Fl.," pp. 49, 110).

all these arrangements for self-fertilization, other pollen for the full fertilization of the stigma below should have to come from another flower and from another root; that it should have to pass the block of its own stigma; to travel to, and to pass through the covering of the close-trapped box formed by the short-styled anthers when the pollen and stigma are mature, before it could ever reach the stigma of the short-styled pistil at all. Nature would obviously be inconsistent with herself, if, after framing such an elaborate set of arrangements favouring self-fertilization, cross-fertilization were in this case, according to Darwin's theory, absolutely necessary for her to fulfil her ordinary law of full and perfect fertility. Nature is scarcely open to the charge of being guilty, in her *natural* course, of such fantastic contrariness.

Thus the short-styled primrose directly contravenes the statement of Darwin that "every known heterostyled plant depends on insects for its fertilization, and not on the wind" ("F. Fl.," p. 259).[1]

We here give (Fig. 2) a representation of the diagram by which Darwin ("F. Fl.," p. 27) indicates the transference of the pollen of each form to the stigma of the other form, which, according to his idea, is necessary in order to effect what he calls "legitimate" union, or full union; and "illegitimate" union, or incomplete union, between the two forms, both of the primrose and of the cowslip.

From all the above considerations we cannot see how it

[1] In both forms of Darwin's diagram ("F. Fl.," Fig. 2, p. 27), the corollas are entirely removed in his figures. In his forms, consequently, the natural difficulties opposed to the transference of the pollen from the long-styled form to the stigma of the short-styles, are obliterated to the eye. In the diagram here attached, the arrow only indicates the goal—the short-styled stigma—which the pollen of the long-styled anthers, in Darwin's opinion, had to reach for its full and legitimate union, though of course it has to pass up its own corolla and down the other.

could be otherwise concluded than that the *short-styled primrose is almost unexceptionally purely self-fertilized.*

The short-styled primroses, moreover, Darwin shows, are, when growing naturally, "*the most productive of the two forms*" ("F. Fl.," p. 36).

We see from the facts above that Darwin has no grounds for his statement, as far, at least, as it bears upon the primrose—except that which his own misleading net

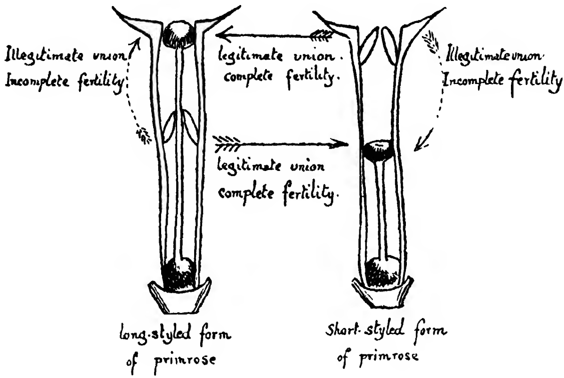

FIG. 2.

experiments afforded him—"that the superiority of a legitimate over an illegitimate union (in Darwin's application of those terms) admits of not the least doubt" ("F. Fl.," p. 38).[1]

[1] When a stigma is fertilized by its "own form" pollen, Darwin calls the union "illegitimate"; when fertilized by the pollen of a flower of a different form, he calls this union "legitimate." Surely, when Nature herself unites stamens and stigma in the same corolla, that is Nature's "legitimate union." To call it "illegitimate union" is merely subserving an unproven theory. Moreover, the origin and application of these terms in this relation arose from Darwin's net experiments by which he was misled ("F. Fl.," pp. 24, 26); experiments which, like his own application of the above terms,

In face of the superior fertility of the almost unexceptionally purely self-fertilized, short-styled form of primrose, we think that Darwin had no evidence to support, but rather *conclusive* evidence against his statement that "one form of primula must unite with the other form in order to produce full fertility" ("F. Fl.," p. 29).

These conclusions at which Darwin arrived so misled those who adopted them after him that Lord Avebury could write, "Mr. Darwin has shown that much more seed is set if pollen from one form be placed on the pistil of the other, than if the flower be fertilized by pollen of the same form even taken from a different plant; nay, what is more remarkable, such unions are more sterile than crosses between some nearly allied, though distinct, species of plants" ("Fl. and Ins.," p. 40); that Mr. Wallace could write in reference to the results of such experiments in the case of the primrose, the following sentence, "The meaning and use of the different forms was quite unknown until Darwin discovered first that the *primroses are absolutely barren* if insects are prevented from visiting them, and then, what is still more extraordinary, that *each form is almost sterile when fertilized by its own pollen*." (The italics are ours.)

"Darwinism," p. 157.

traversed in their result the absolute arrangements of Nature. Nor have we perhaps arrived at that perfect and complete knowledge in the matter, as to venture to appear wiser than Nature herself, and so to divorce what she has *naturally*, and so "legitimately" joined together. Such forced transpositions in terminology of the arrangements of Nature should, we think, for the sake of clearness, and to avoid all appearance of subserving a theory, be most carefully eschewed. For Darwin to set up as a judge in Nature's divorce court, and to give a decision for divorce when the evidence against the legitimacy—productiveness being Darwin's criterion of legitimacy—of the union of the occupants of the same corolla was only the forsworn evidence of his own net, and when many a primrose testified, if Darwin had only interpreted their testimony correctly, to the legitimacy of their union, transgresses a little, we think, the bounds of modesty.

Mr. Wallace then adopts the ingenious supposition of Darwin, which we have already quoted above, from Lord Avebury, and accounts for the superior fertility of the short- to the long-styled, by saying, "The wild, short-styled plants were found to be almost always more productive of seed since *they must be all fertilized by the other form;* whereas the long-styled plants might often be fertilized by their own form." (The italics are ours.) Now, such an affirmation is absolutely contrary to all the natural facts connected with those flowers. "Darwinism," p. 158.

The long-styled primroses, on the other hand, though almost entirely, if not absolutely, self-fertilized, as we have seen by the entire absence of all visitation by insects except the tiny Thrips, and by the general position of the pollen on the bottom and lower half of the stigma, yet would be slightly more exposed to cross-fertilization by the wind on account of the position of their stigma at the mouth of the corolla by the pollen of the short-styled, whose anthers are also exerted from their corolla. The more papillose character of the long-styled form of stigma would also slightly conduce to favour some possible cross-fertilization of this form. If such is the case, still, as the produce of seeds in the long-styled form, when naturally grown, is inferior to that of the uncrossed, short-styled primrose, Darwin's theory, "that one form of primrose must unite with the other form in order to produce full fertility," is disproved by the occasionally-possibly-crossed, long-styled form remaining inferior in productiveness to the uncrossed short-styled one.

CHAPTER VII

DARWIN'S STATEMENT THAT THE VISITS OF INSECTS ARE "ABSOLUTELY NECESSARY" FOR THE FERTILIZATION OF THE COWSLIP, UNTENABLE.

The same conclusion as to fertilization, as far as insects are concerned, applies with almost equal force to the cowslips as to the primroses. If Darwin had not said that he had "often seen humble-bees sucking the flowers in a proper manner" ("F. Fl.," p. 22), and again, "the cowslip is *habitually* visited during the day by the larger humble-bees and at night by moths" (p. 56—the italics are ours), we should not, in our comparison above of the cowslip with the primrose, have qualified with "almost" the above statement at all, as in our experience we have found the cowslip to be as equally unvisited by insects as the primrose. The tube of the corolla of the cowslip is of the same average length as that of the primrose. The anthers are situated, and incline with their apices towards the centre of the corolla, as in the primrose. They fail, however, in a large number of instances, in forming so close a box over the stigma as in the case of the primrose. This, we think, probably arises from their being more subject to the buffeting of the wind, and so very frequently they become displaced and separated. We have passed through acres and acres of cowslips where there were tens of thousands upon tens of thousands of cowslip flowers, and have not seen a single humble-bee, or butterfly, or moth, or Anthophora, or

Bombylius upon any one of the flowers. We have done this in different places and in different situations, sometimes in perfectly open pasture lands, and sometimes where engirdled with woods. We only saw two humble-bees even flying in a field of twenty acres, which was positively almost yellow with cowslips. We visited the field on several occasions, and in successive years, with no greater success. This would not have been the case had the flowers been at all attractive to them, or usually visited by them. On some occasions we have seen an occasional humble-bee visiting the dandelion which grew amongst the cowslips, but it would fly from dandelion to dandelion, and take no notice whatever of any of the cowslips. Others, we admit, may have seen such occasional visits of humble-bees; but we cannot but think that such visits to the flowers are, in the experience of observers generally in the fields, very exceptional indeed, and that they would be far from giving the slightest support to Darwin's statement that "the cowslip is *habitually* visited by the larger humble-bees" ("F. Fl.," p. 56. The italics are ours).

Moreover, there is only one humble-bee (*Bombus hortorum*) that could reach the nectar of the cowslip with any facility. The rest would necessarily, on account of the length of the corolla tube, be forced to bite through the middle of the tube to reach the nectar. Darwin, after saying what we have quoted above, continues, "though they sometimes bite holes in the corolla" ("F. Fl.," p. 22). We have never noticed such a case. In such a case no cross-fertilization would be effected. All such humble-bees would necessarily, from the early season of the year, be, with few exceptions, the female humble-bees alone. Such female humble-bees are then few indeed in comparison with the vast number of cowslips in many pastures, and especially when in this case the visits would be limited almost to a single species, *Bombus hortorum*. If exceptional worker

humble-bees were abroad, they would necessarily be obliged, from their shorter tongues, if they visited the flowers, to bite through the tube of the corolla, as Darwin states that humble-bees sometimes do.

The only long-tongued bee that we have seen sucking the flowers is the *Anthophora pilipes*. On one occasion, and one occasion only, we saw two specimens of this bee visiting the flowers. This bee, as we have noticed before, is a comparatively rare insect, as it is a solitary, and not a social, bee, and is not met with in every district. No great influence could be exercised by them in the cross-fertilization of the flowers.[1]

These instances, after lengthened and close observation, are all the living insect-life which we have seen upon the cowslip. Cases of other insects may be met with by other observers, but we feel sure, from our own experience, that such cases will be with them most exceptional.

We have taken care with the cowslip, as well as in the case of the primrose, to make our visits on the most propitious days, when the mornings were warm and calm, and the sun was shining—on the days and at the hours on which insects are most abroad; yet we have failed to see a single instance of such a visit to the flowers by humble-bees.

Darwin, moreover, attaches this "habitual" visitation of the cowslip to the moths as well as to the humble-bees. "The cowslip is habitually visited during the day by the larger humble-bees, and at night by moths" (p. 56). Only one instance of such visit is given us in support of this statement. "No doubt moths likewise visit the flowers,"

[1] On one occasion we saw and caught upon the flowers five short-tongued bees (*Andræna Gwynana*). These were feeding on the pollen of the short-styled cowslip. their tongues being far too short to reach the nectar. They consequently would be no agents in effecting cross-fertilization, as they would not visit the long-styled form at all, the pollen in these forms being far too low for them to reach.

Darwin says, "as *Cucullia verbasci* was caught in the act" ("F. Fl.," p. 22). Butterflies and day-flying moths we have never seen visiting the flowers in the field, nor does Darwin mention any of such day-fliers as so seen, and nothing has been discerned in the nature of a cowslip to make us suppose that it would present greater attractions to night-flying Lepidoptera than it does to the day-flying ones. To evolve from an isolated occurrence the habitual occurrence of such nocturnal visits, ignoring the mass of evidence that speaks against it, can scarcely be considered a logical deduction. We feel assured, however, that Darwin did not arrive at this conclusion from any general observations in the fields, for we should not have had this solitary instance alone produced if he had seen others visiting the flowers. To this general inference Darwin was almost driven from the negative results in fertilization which he obtained in his experiments with cowslips under his most misleading net.

Under the influence of those misleading experiments with the "umbels of cowslips," which we have already recorded in Chap. IV.—the sterilizing influence of Darwin's net—in which 24 umbels of short-styled cowslips under the net produced only 1¼ grains' weight of seed, and 74 umbels of long-styled cowslips produced none at all, whilst uncovered cowslips outside the net produced abundantly, Darwin says, "We see *thus* that the visits of insects are absolutely necessary to the fertilization of the cowslip" ("F. Fl.," p. 22. The italics are ours). This sentence indicates the source of Darwin's conclusion.[1] It was

[1] One other instance Darwin cites in support of this opinion. After giving that of the umbels, he continues, "It is scarcely necessary to give any additional evidence, but I may add ten pots of polyanthuses and cowslips of both forms, protected from insects in my greenhouse did not set one pod, though artificially fertilized flowers in other pots produced an abundance." That Darwin should expect any other result from cowslips "protected in a greenhouse" seems

consequently necessary for Darwin to suppose from one solitary instance the *habitual* visits of nocturnal Lepidoptera. The case of the cowslip as thus treated by Darwin is in a close parallel with that of the primrose. When all other instances of cross-fertilization of that flower failed him, Darwin says, "*Hence* its fertilization must depend almost exclusively upon moths" ("F. Fl.," p. 56). This, too, was said when not even a single moth was known to visit the primrose. Both conclusions of Darwin were founded upon his untenable theory about heterostyled flowers, "as both species" (primrose and cowslip), Darwin says, "are heterostyled, their complete fertilization depends on insects" ("F. Fl.," p. 36).

But even if the evidence were different from what it is, and it was allowed that the cowslip was cross-fertilized to some considerable extent, that very fact would not advance Darwin's theory of the absolute need for reciprocal fertilization of the two forms, as in his experiments ("F. Fl.," Table 6, p. 25), the *short-styled* cowslip crossed by pollen of the *long-styled* produced 44 grains' weight of seed; and the *long-styled* cowslip fertilized by "own form pollen" produced 42 grains' weight.

This difference between the crossed flowers and the other flowers with their "own form" pollen was scarcely more than just noticeable, and in the flowers when growing wild Darwin noticed that the "*short-styled* flowers *naturally* produced more seed than the *long-styled*." Moreover, in the very same table, he tells us that the short-styled cowslip from its "own form" pollen produced 30 seeds. In face of the above facts, it seems surprising that Darwin should arrive at the conclusion expressed in his statement, "short-styled cowslips, when insects are excluded, are extremely barren" ("F. Fl.," p. 235).

extraordinary when he so often alludes to the injurious effect on flowers when "unnaturally treated" ("F. Fl.," p. 210).

As there is no adequate evidence at all that the thousands upon thousands of wild cowslips in the fields are *habitually* visited by any insects sufficiently long-tongued to reach the nectar and so to effect in them cross-fertilization, they also must be capable of self-fertilization, for, as H. Müller has well observed, "flowers which are rarely visited must be capable of self-fertilization, otherwise they would quickly become extinct."[1]

H. Mülle "Fert. of Fl.," 385

[1] The familiar lines of Shakespeare—

> "Where the bee sucks, there suck I;
> In a cowslip's bell I lie;
> There I couch when owls do cry,"

have closely associated the bee with the cowslip in the fancies of many persons, and the lines have been so cited in a botanical writing. But Shakespeare makes his fairy spirit say that "he feeds where the bee feeds" and "*couches in the cowslip*."

CHAPTER VIII

DENATURALIZING INFLUENCE OF THE NET ON PRIMULAS

If we needed any further illustrations of the denaturalizing influence of the net, beyond what we have already produced, we have *conclusive* instances afforded us by other experiments of Darwin on the *Primulas*. "There is another point," Darwin says, "which deserves notice, namely, the relative degree of infertility in the several species of the long-styled and short-styled primulas, when both are illegitimately fertilized. If we call the number of seeds per capsule produced by the illegitimately fertilized long-styled flowers 100, the seeds from the illegitimately fertilized short-styled flowers will be represented in *Primula veris* (the Cowslip) by 71, and in the *Primula vulgaris* (the Primrose) by 36" ("F. Fl.," p. 48). In the cases of 7 other primulas experimented on as given in the table on "Forms of Flowers," p. 48, six of these short-styled primulas produced few seeds, and some of them very considerably fewer in comparison with the long-styled; there was one exception only to this result. That occurred in *Primula auricula*, in which flower the short-styled exceeded the long-styled in productiveness. "We see thus," Darwin says, "that with the exception of *P. auricula*, the long-styled flowers of all 9 species are more fertile than the short-styled flowers, when both forms are illegitimately fertilized" ("F. Fl.," p. 48).

The table referred to above we give here. The seeds

per capsule produced by the illegitimately fertilized long-styled flowers are reckoned as 100. The illegitimately fertilized short-styled flowers are represented by the following numbers :—

Primula veris (cowslip) . .	71	*P. sikkimensis*	57
P. elatior (probably too low)	44	*P. cortusoides*	93
P. vulgaris (probably too low)	36	*P. involucrata*	74
P. sinensis	71	*P. farinosa*	63
P. auricula	119		

This result was exactly the opposite to the conclusion to which Darwin had come from his examination of primroses and cowslips when grown *naturally in the open air.* "Looking to these trials" (naturally in the open air) "made during two successive years on a large number of plants," Darwin says of the cowslips, "we may safely conclude that the short-styled form of cowslip is more productive than the long-styled form." Of the primrose, Darwin says, "The primrose resembles the cowslip in the short-styled plants being the more productive of the two forms" ("F. Fl.," pp. 20, 36).

Darwin, in thus contradicting as above the results which he found in primroses and cowslips, and "some other species of *primula*," when *growing naturally* by the results he found under the net, was under the impression that the two forms of primroses, when growing wild, had necessarily —as he considered the two forms sexually distinct—been according to his view reciprocally, and so in Darwin's nomenclature, "legitimately" fertilized. This view, as we have seen, is quite disproved by the facts connected with the primrose. We have consequently a great denaturalizing effect produced on these short-styled flowers under the covering of the net. The net seems to have had a more pernicious influence on the short-styled flowers than upon the long-styled.

The only way in which we would attempt to account

for it is the sensitiveness of the stigmas. Darwin tells us that "the pollen, when once mature, may be kept for weeks, or even months," and that "there are cases where plants in their stigmatic portions are sometimes struck with sterility whilst the anthers remain perfect. Gärtner has described three cases in this unusual condition." This sensitiveness of the stigma may not improbably be the correct explanation of this partial sterilizing under the net of the short-styled *Primulaceæ* in comparison with the stigmas of the long-styled. The short-styled stigmas were covered not only by the net, but by their own corollas also, whilst the long-styled stigmas were more exposed, having only the covering of the net. If such be not considered a sufficient cause of this failure of the short-styled flowers, we do not attempt to suggest any other alternative one, but prefer to leave it to more expert vegetable physiologists to explain.

"Animals and Plants under Domestication," pp. 148, 149.

Whatever be the cause, these instances, as recorded by Darwin, at least exemplify how utterly unreliable experiments made under a close-meshed net are as to giving results similar to those which are produced under natural conditions. Moreover, it is particularly noticeable that the short-styled primrose, which, when growing wild, has been shown to be (according to Darwin's nomenclature) illegitimately fertilized, and whose seeds in such wild state "weighed exactly twice as much as those of the long-styled," stands lowest here on the list, with an average of 36 seeds only, in comparison with the long-styled flower with its average of 100 seeds. "I may remark," Darwin says, "that of the four kinds of unions, that of the short-styled illegitimately fertilized, with its own form pollen, seems to be the most sterile"! ("F. Fl.," p. 32).

CHAPTER IX

SPECIAL POSITION OF THE PRIMROSE AS TO DARWIN'S THEORIES ABOUT HETEROSTYLED PLANTS

DARWIN affirms that the individual plants of the primrose and cowslip and of the members of the *Primulaceæ* "are divided into two sets, which cannot be called distinct sexes (for they each have their own stamens and pistils), yet they are as male and female in quadrupeds to a certain extent sexually distinct, for they require reciprocal union for perfect fertility" ("F. Fl.," pp. 24, 28). He also further asserts that "illegitimate unions of the heterostyled species closely, and in many points, represent hybrid unions between distinct species, as in both cases we meet with every degree of sterility, from very slightly lessened sterility to absolute barrenness" ("F. Fl.," pp. 239, 240). These two propositions are absolutely and fully disproved by the short-styled primrose.

We see, thus, that the *primrose* holds a *special position* in reference to several theories of Darwin about heterostyled plants, which, except for it, could scarcely be disproved, or be shown to be built on misleading net experiments. The same could not perhaps be so absolutely shown, as far as we are aware, by any other members of the *Primulaceæ*, nor by any other heterostyled dimorphic flower.[1]

[1] We say this, though we think that other Primulas, like the

The primrose disproves the following theories of Darwin,

that "every known heterostyled plant depends on insects for fertilization and not on the wind" ("F. Fl.," pp. 55, 259, 310);

that "one form of Primula must unite with the other form, in order to produce full fertility" ("F. Fl.," pp. 49, 56);

that "the superiority of a legitimate over an illegitimate union admits of not the least doubt" ("F. Fl.," p. 28);

that "the parallelism is wonderfully close between the effects of illegitimate and hybrid fertilization" ("F. Fl.," p. 242);

that "plants have been rendered heterostyled to ensure cross-fertilization" ("F. Fl.," pp. 30, 258; "Cr. and S. F.," p. 383);

and, lastly, that "heterostyled flowers stand in the reciprocal relation of different sexes to each other" ("F. Fl.," pp. 2, 28, 245).

Such unnatural results in the case of the primrose and cowslip under a close-meshed net, as those given in the preceding pages—first, the long-styled flowers being more productive in seeds than the short-styled ones, when they are each cross-fertilized; secondly, the same result occurring when they are each fertilized by their "own form" pollen; and next, the short-styled flowers when illegitimately fertilized by their "own form" pollen being the most sterile of all—quite invalidate the value of experiments conducted under such a method, and render all conclusions in respect to other heterostyled *Primulaceæ* drawn from such experiments eminently unsatisfactory, and even scientifically worthless. Nor can they fail to render similar conclusions drawn from exactly similarly conducted

cowslip or the polyanthuses of our gardens, bear similar, and perhaps equal testimony.

experiments on the other heterostyled dimorphic and trimorphic forms, such as *Linum perenne* and *Lythrum salicaria*, equally questionable and perhaps equally scientifically worthless.[1]

H. Müller was so far led aside by these experiments of Darwin, that in his introduction to his "Fertilization of Flowers" he says: "The results of Darwin's investigations Page 10. proved that in heterostyled plants the regular crossing of separate individuals was absolutely essential for the maintenance of the species."

[1] Darwin, writing to Professor Hildebrand (July 28, 1863), says, "I was told that the most eminent French botanists in Paris said that my paper on Primula was the work of imagination, and that the case was so improbable that they did not believe in my results" ("Life of Darwin," vol. iii., p. 305).

CHAPTER X

AXELL'S OPINION AS TO FERTILIZATION

THE eminent botanist, Axell, has very different views from Darwin as to the amount of self-sterility to be met with in flowers, and as to the superior benefits of cross-fertilization. He holds the opinion that the self-fertilization of flowers under equal conditions in a state of nature is both the natural fertilization and the most productive; and that "the most perfect flowering plants are those which regularly fertilize themselves." It is difficult to find in nature flowers which give absolute evidence for the one opinion or the other; evidence which cannot be gainsaid or contradicted. Axell's views, however, in contrast to those of Darwin, are as to heterostyled *Primulaceæ* thus absolutely supported by the short-styled primrose. Every cleistogamous flower-bearing plant is also an absolute witness to the validity generally of the self-fertilization of flowers. It might almost be said that the vast majority of flowers—especially the inconspicuous flowers—though not giving any absolute evidence, yet give strong confirmatory witness to self-fertilization being the natural fertilization, by their not being visited by bees, who are the chief agents in cross-fertilization, by the more or less close approximation in which the stamens and pistils are generally placed in the flowers in which they both appear. For what other purpose

H. Müller, "Fert. of Flowers," p. 587.

can Nature have so designed the usual order of the arrangements of the flowering parts? It cannot be in order that bees may thus effect cross-fertilization, as a similar arrangement is found both in inconspicuous flowers which are never visited by bees, and in those which are visited by them, and the former far preponderate in number over the latter. Darwin was misled as to the potency of insects by his own method of cross-fertilizing. He looked upon his own method of applying the pollen as supplying the place of insects, and as their equivalent in natural operations; but it was more. Professor Henslow well observes, "The results which Darwin's crossings yielded were more marked because plants are never so carefully crossed in Nature, nor self-fertilization so carefully prevented, as was the case in his operations. By his experiments, the more unalloyed influence of crossing brought about a much more enhanced stimulus than ever occurs in the wild state." Even the bees, to whom Darwin assigns "Floral the chief agency in effecting cross-fertilization, are far more Structures," p. potent agents in effecting the self-fertilization of flowers. 316. The benefit of bees, and the Hymenoptera, etc., generally arises rather from their disturbing the pollen grains in the immediate vicinity of the pistil of each flower they visit, than from carrying a few grains from one plant to another, and even then parting probably with only a very small fraction of that which they may chance to carry. Moreover, as Darwin says, "Insects usually search a large number of flowers on the same plant before they fly to another, and this is opposed to cross-fertilization. A cross between flowers on the same plant does no good or very little good. The advantage of a cross depends wholly on plants differing somewhat in constitution" ("Cr. and S. F.," pp. 254, 390, 449). Both processes doubtlessly take place in all flowers frequented by bees, etc., but to minimize the one, and to confine such visits beneficially to their effecting

cross-fertilization, is pressing too much in one direction their influence in Nature.[1]

Axell allows the beneficial influence of cross-fertilization by bees and insects as a secondary agency. Such secondary agency might be constantly occurring. The pollen of a flower might be imperfectly developed or imperfectly matured from various causes; from the position of the flower in field or hedge, on stem or branch, as being more exposed to injury from wind or weather; from its growing under any shade, and so being deprived more or less of the solar rays or dew; from the character of the soil, or from the flower's own internal defective growth. From all these, and many other accidental and natural causes, this might constantly arise. In such cases pollen from flowers more favourably situated, and consequently more healthy and vigorous in growth, and so with anthers more matured, would, by the conveyance of bees and other hymenoptera, moths and butterflies, act most beneficially. In such cases, the pollen conveyed by them would exert what Darwin calls a "prepotent" influence over the legitimate influence of the pollen of its own flower, but its "prepotency" would be usually limited to such weaker cases amongst the flowers.[2]

[1] Such pressing is frequently met with in Lord Avebury's "Flowers and Insects." In many of his descriptions we read, "If the flowers are not visited by insects, and so cross-fertilization does not occur, then the flowers can fertilize themselves" (pp. 73, 81, 86, etc). In our opinion, the course of nature would be more correctly stated by "these flowers are self-fertilizing, but, if visited by insects, they may be cross-fertilized." In H. Müller's "Fertilization of Flowers," cross-fertilization is continually begged. We meet over and over again in his pages with such statements as the following: "In the absence of insects, self-fertilization—'may'—'usually,' 'always'—takes place." This, too, in very many cases where no absolute proof exists that any insect influence has precedence of the influence of the flower itself ("Fert. of Fl.," pp. 76, 82, 416, 424, to cite only a few instances).

[2] We do not ourselves believe that the floral world in its ordinary course is utterly dependent upon insects, as we have been assured by

some writers, but rather that it is by insects, through their seeking for food, beneficially assisted. Such a statement as the following, by Lord Avebury—"It is not too much to say that if, on the one hand, flowers are in many cases necessary to the existence of insects, insects, on the other hand, are still more indispensable to the very existence of flowers" ("Fl. and Ins.," p. 5),—seems to us to diverge very far indeed from, and to reverse, the facts as found in Nature. All purely nectar-feeding insects, as bees, fossores (diggers), butterflies, and moths, which are the acknowledged chief agents in effecting cross-fertilization, would die out in less than a single year if they had no food provided for them by the flowers. The inconspicuous flowers generally are acknowledged by all to be self-fertilized. Nor do we see any sufficient reason for placing the more conspicuous and gaily coloured flowers—very many of which, as well as the primroses and cowslips, are quite unvisited by bees, and very many others only very partially visited by them—in a different category from the inconspicuous as to their general independence of insects for their existence.

CHAPTER XI

THE INFERIORITY OF SELF-FERTILIZED TO CROSS-FERTILIZED SEEDLINGS IN DARWIN'S EXPERIMENTS DUE TO THE DISADVANTAGEOUS CONDITIONS TO WHICH THE FORMER WERE SUBJECTED

BUT it might be objected that Darwin, in his experiments detailed in his volume, "Cross- and Self-Fertilization of Flowers," has shown that seedlings, raised from the seeds of cross-fertilized flowers, are more vigorous than seedlings raised from the seeds of self-fertilized ones. On this subject of seedlings we do not propose to enter at any length, as it is beyond our present purpose. We shall merely state our reason for considering that the method of Darwin's experiments there detailed not only renders questionable, but rather vitiates and renders worthless the results and conclusions at which Darwin arrived.

Now, the objection in this case is not so much from the net itself, for the self-fertilized parents and the cross-fertilized parents were both under the net. It is the method adopted in these experiments which in our view vitiates the results.

"My experiments," Darwin says, "were tried in the following manner. A single plant, if it produced a sufficiency of flowers, or two or three plants, were placed under a net stretched on a frame. On the plants thus protected several flowers were marked and were fertilized

with their own pollen; and an equal number on the same plants were at the same time crossed with pollen from a distinct plant. The crossed flowers had not their anthers removed" ("Cr. and S. F.," pp. 10, 11).

In these experiments, consequently, the cross-fertilized plants had a great advantage. The self-fertilized plants had only their own pollen, and that developed under a net, to fertilize them; but the cross-fertilized had not only their own pollen—for, as we have seen above, their anthers were not removed—but pollen from another plant applied to them as well, *and that too grown naturally outside the net;* for Darwin wished, by leaving the flowers their own pollen, and at the same time crossing them with other pollen, "to make the experiments as like as possible to what occurs under Nature, with plants fertilized by the aid of insects" ("Cr. and S. F.," pp. 10, 11).

The cross-fertilized had, consequently, two sets of pollen to choose between, and whichever happened to be most in its prime, that would exercise a "prepotent" influence in the fertilization. But the flowers fertilized with their own pollen had no other pollen but their own to depend upon, and none to choose between. It must be their own pollen, and that developed under a net, which must fertilize them, or none at all.[1]

[1] In some instances the disadvantage in the case of those fertilized with their own pollen went even further. "In some few cases of spontaneously self-fertile species, the flowers were allowed to *fertilize themselves* under the net." In such cases, an inferior fertilization would naturally follow when the full influence of the wind was excluded. On the other hand, a still further advantage was given to some of the crossed. "In still fewer cases *uncovered* plants were allowed to be freely crossed by the insects which incessantly visited them" ("Cr. and S. F.," p. 11. The italics are ours). These plants were uncovered. This was done, though the seedlings, which were raised from the seeds produced from the two sets, were afterwards to be compared in order to estimate the potency of self- and cross-fertilization.

Such a system of experiments evidently gave to the *cross-fertilized flowers a very great advantage* over the self-fertilized ones, and consequently a very great advantage for the production of better-developed seeds, and for the stronger growth and vigour of the seedlings raised from them.

It is no wonder that under such conditions, that the seedlings of the self-fertilized were, in some instances, in comparison with the others "somewhat weakly in constitution" ("F. Fl.," p. 31), and that, as in the case of *Primula sinensis*, they were "somewhat dwarfed in stature, and that some had so poor a constitution that the majority perished before flowering" ("F. Fl.," p. 217).

So greatly was Darwin misled by his method of experimenting with seedlings that he could say, "It is hardly an exaggeration to assert that seedlings, from an illegitimately fertilized heterostyled plant, are hybrids formed within the limits of one and the same species" ("F. Fl.," p. 242). Darwin, in his introductory remarks to his *Cross- and Self-Fertilization of Plants*, when he defends the method he had adopted in comparing the relative fertility of cross- and self-fertilized seedlings, merely meets the objections raised to the injuriousness of a net on the health and fertility of the plants by the following sentence, "Even if the net were slightly injurious, and certainly it was not so in any high degree, it would not have vitiated my experiments: for in all the more important cases the flowers were crossed as well as self-fertilized under a net, so that they were treated in this respect exactly alike" ("Cr. and S. F.," p. 22). So far as "being under the net, and being fertilized under the net," the flowers, as we have already observed, were treated exactly alike. But there the alikeness ceases. The mere presence of the net—except so far as it hindered the perfect maturation of the pollen of the self-fertilized—is not the question here at all. The crucial objection in

these experiments to Darwin's method, which Darwin most singularly fails to notice, is, that the crossed flowers had two pollens to choose between, and one of them *grown naturally* outside the net, and that the other had only its own pollen, and that developed under the net.[1] This is a specially important point in the consideration, as Darwin tells us "that the good effects of cross-fertilization"—here the cross-fertilization is with pollen naturally grown in contrast to that of the self-fertilized grown under the net—"are transmitted by plants to the next generation, and to many succeeding generations. But this may merely be that crossed plants of the first generation are extremely vigorous, and transmit their vigour like any other character to their successors" ("Cr. and S. F.," p. 414). It is this inequality of conditions under which the seeds were produced, whence the seedlings were grown, which, in our opinion, vitiates and renders scientifically worthless the results which Darwin obtained.

Notwithstanding the great inequality of conditions under which the self-fertilized seedlings were produced, yet we find that in many instances, though thus handicapped, the self-fertilized seedlings surpassed the cross-fertilized, either in height, weight, or fertility, the points in which Darwin expressly compared them.

With *Mimulus luteus*, Professor G. Henslow says, "a strong, self-fertilizing form arose under Darwin's cultivation, so that it was quite useless to continue the experiment after seven generations, as the self-fertilized form entirely

[1] Even in the cases which seem to have been conducted in a greenhouse—Darwin's initial experiments with *Mimulus luteus* and *Ipomæa purpurea* ("Cr. and S. F.," pp. 9, 10)—the crossed flowers had not only the advantage of the two kinds of pollen, but, even if the pollen used for crossing was grown in the greenhouse, pollen so grown would still have the chance of being better matured than that of the self-fertilized flowers, in which it was grown under a net as well.

Popul. Sci. Rev., v. 3. New Series.

surpassed the intercrossed." A similar superiority in the self-fertilized occurred in *Ipomœa*. "The later generations,' Darwin says, "of Mimulus are not included as a new tall (self-fertilized, p. 240) "variety then prevailed on one side alone, so that a fair comparison between the two sides was no longer possible" ("Cr. and S. F.," p. 239). "With Ipomœa the variety called "Hero" has been excluded for nearly the same reason" ("Cr. and S. F.," p. 239). Prof. G. Henslow shows that the self-fertilized gradually came on an equality with, and finally surpassed the cross-fertilized.

"Floral Structures," p. 322.

In many others, especially in *Eschscholtzia Californica*, *Nicotiana tabacum*, *Pisum sativum*, a similar superiority of the self-fertilized seedlings in several aspects appeared.

So great was the inequality of the conditions under which the two sets of seedlings were produced, that all discussion of particular instances of results seem absolutely profitless. Darwin's results, as given in his Tables (pp. 238-252), cannot be accepted as any reliable indication whatever of what takes place when the flowers grow naturally in their wild state, in their natural habitats, and under equal conditions of fertilization.[1]

Yet on the results of these experiences Darwin mainly relies for the following conclusion: "From the effects," Darwin says, "of cross-fertilizing flowers which are self-fertile, and have not had their anthers removed, we may conclude that pollen, brought by insects, or by the wind from a distinct plant will generally prevent the action of pollen from the same flower, even though it may have been applied some time before;[2] and thus the intercrossing of

[1] In Table A, "Cr. and S. F.," pp. 240-243, out of 98 experiments recorded, only 21 of these are on English plants, the remaining 77 are on foreign plants. Even of the English plants, Darwin says, "Most of the plants on which I experimented were grown in my garden, or in pots under glass" (p. 456).

[2] This subject will be treated in the next chapter.

plants in a state of nature will be greatly favoured or *ensured*" ("Cr. and S. F.," p. 400. The italics are ours).

From this method of experimenting, Darwin drew what he calls, "two other important conclusions." One, that the advantage of cross-fertilization follows from two distinct individuals, "having been subjected during previous generations to different conditions, or to their being varied in a manner commonly called spontaneous, so that in either case their productive organs have been in some degree differentiated. The other that the injury from self-fertilization follows from want of such differentiation." "These two propositions," he says, "are fully established by my experiments."

Let us now examine the case which he gives us in connection with, and in illustration of, these propositions ("Cr. and S. F.," p. 448).

"Plants of mimulus which had been self-fertilized for the seven previous generations, and had been kept all the time under the same conditions, were intercrossed one with another, the offspring did not profit in the least by the cross." Then again, Darwin says, "*Mimulus* offers another instructive case, showing that a benefit of a cross depends on the previous treatment of the progenitors; plants which had been self-fertilized for the eight previous generations were crossed with plants which had been intercrossed for the same number of generations, all having been kept under the same conditions as far as possible; seedlings from this cross were grown in competition with others derived from the same self-fertilized mother-plant crossed by a fresh stock; and the latter seedlings were to the former in height as 100 to 52, and in fertility as 100 to 4." Is this result other than what might have been anticipated, viz. that fresh, naturally grown pollen would have a far stronger influence in producing well-developed seeds than pollen from plants which, during eight generations, had been

during the flowering time more or less under protection? Yet Darwin quotes these experiments to show the injury from self-fertilization when the two flowers had been grown under the same conditions, and the benefit of cross-fertilization when the parents had been subjected to different conditions. We must have very different evidence from that which Darwin gives us here before we can acknowledge that "these two propositions have been fully established by his experiments." Outside such invalid experiments there is no evidence whatever for his theory.

If this idea of Darwin is really true in Nature, any effective cross-fertilization would be very rare. Two plants growing, we will say, in the same clump, or even on the same kind of soil, would not be affected in any beneficial way by the visit of bees. The agency of bees, to which Darwin is wont to assign such great importance in cross-fertilization, would, by his own showing, be reduced to a minimum unless they visited flowers, on the same flight, on very different soils, or with some other very marked difference of condition. And so their influence, as we stated our belief in the preceding chapter, would be limited to the weaker cases amongst the flowers.

This difficulty to his favourite theory, Darwin allows, and endeavours to obviate. "But it may be said," Darwin suggests, "granting that changed conditions act on the essential organs, how can two or more plants, growing close together, either in their native country, or in a garden, be differently acted on, inasmuch as they appear to be exposed to exactly the same conditions." He experimented with a wild foxglove (*Digitalis purpurea*). Some flowers "were self-fertilized, and others were crossed with pollen from another plant growing within two or three feet's distance. The crossed and self-fertilized plants raised from the seeds thus obtained, produced flower stems in number as 100 to 47, and in average height as 100 to 70. But how

could their essential organs have been differentiated by exposure to different conditions?" The reply which he makes is, "Seeds are often widely dispersed by natural means, and one of the above two plants, or one of their ancestors (!) may have come from a distance, from a more shady, or sunny, dry, or moist place, or from a different kind of soil containing other organic or inorganic matter" (pp. 452, 453). This experiment, as all his experiments, being necessarily conducted under a net, Darwin need not have travelled so far afield for an explanation of the results he met with. His own net had supplied what he went so far afield to seek. The pollen of the self-fertilized was from "a more shady situation," *i.e.* from a flower matured under his net; and the pollen of the cross-fertilized from "the more sunny" situation, being grown uncovered. The differentiation Darwin had himself created in these two closely neighbouring flowers; all that this experiment showed was, that pollen, naturally grown, was prepotent over that which was grown under artificial protection. It was no matter of ancestry. The crossed flower had, moreover, the two pollens to choose between, and had also the pollen directly applied to it, but the other was self-fertilized. The two conditions were very far indeed from being analogous.[1]

[1] This experiment is given us more at large on pages 82–84. "I covered," Darwin there says, "a plant growing in its native soil in North Wales with a net, and fertilized six flowers with pollen from a distinct plant growing within the distance of a few feet. The covered plant was occasionally shaken with violence, so as to imitate the effects of a gale of wind, and thus to facilitate as far as possible self-fertilization. It bore 92 flowers, and of these (besides the dozen artificially fertilized) only 24 produced capsules, whereas, almost all the flowers on the surrounding uncovered plants were fruitful." It was from the seeds of these self-fertilized capsules that he grew his seedlings, and made the comparison which we have given above of the superiority of the crossed seedlings to the self-fertilized ones. Darwin says of these self-fertilized seedlings, which were 17 in

Relying upon these experiments, when the plants raised from the seeds of self-fertilized parentage "were markedly inferior in many ways to their cross-fertilized brethren," Darwin says that "it is an astonishing fact that certain plants, such as the Foxglove (*Digitalis purpurea*), and the Common Broom (*Sarothamnus scoparius*), which have been naturally cross-fertilized for many, or all, previous generations, should suffer to such an extreme degree from a single act of self-fertilization" ("Cr. and S. F.," p. 443). We think, rather, that the fact would have been more astonishing if the self-fertilized plants had not failed *at once* in comparison with the cross-fertilized, under the method which he adopted. What seems to us still more astonishing is that Darwin should base on the mere fact of the results obtained by his method the general conclusion that self-fertilization is injurious. "Several plants," Darwin says, "such as *Reseda* and *Eschscholtzia*, must have been crossed during a long series of previous generations, and the artificial crosses in my experiments cannot have increased the vigour of the offspring beyond that of their progenitors. Therefore the difference between the self-fertilized and crossed plants raised by me cannot be attributed to the superiority of the crossed, but to the inferiority of the self-fertilized seedlings, *due to injurious effects of self-fertilization*" ("Cr. and S. F.," p. 440. The italics are ours).

We are, therefore, quite unable to accept Darwin's conclusions, deduced from experiments conducted under such a method as that expressed in his last chapter (general results) of his *Cross- and Self-Fertilization of Plants*. "The first and most important of the conclusions which may be drawn from the observations given in this volume is," Darwin says, "that generally cross-fertilization is

number, "these had such poor constitutions that no less than 9 died in the course of the winter and spring; all but one of the crossed seedlings survived."

beneficial, and self-fertilization often injurious. The truth of these conclusions is shown by the difference in height, weight, constitutional vigour, and fertility, of the offspring from cross- and self-fertilized flowers" ("Cr. and S. F.," p. 439).

Still less could we allow "that such a benefit from cross-fertilization has now been *firmly established* by the *proved* superiority of plants of crossed- over those of self-fertilized parentage" ("Cr. and S. F.," p. 372. The italics are ours).[1]

[1] It is necessary, on many occasions, in reading Darwin's books, to be on one's guard against accepting such statements as the following:— "We should bear in mind how important an advantage it has been *proved* to be to many plants, though in different degrees and ways, to be cross-fertilized" ("F. Fl.," p. 261, etc.). Such supposed proofs were obtained from his net experiments.

The primrose, singularly enough, is actually never mentioned in the volume of "Cross- and Self-Fertilization of Plants," though it occupies so important a position, as we have seen, in Darwin's "Forms of Flowers." This is a very singular omission indeed, as not only the cowslip is introduced in these experiments, and in a dozen different allusions, but all the other primulas as well, as *Elatior*, *Sinensis*, *Scotica*, etc.

But notwithstanding that omission, Darwin, in his "Cross- and Self-Fertilization" volume, makes this general assertion concerning the Primulaceæ: "The Primulaceæ seem eminently liable to suffer in fertility from self-fertilization" ("Cr. and S. F.," p. 319). The primrose, as we have already seen, as a test flower, holds a special position in reference to the question of cross- and self-Fertilization, and absolutely contravenes for itself, and, in our opinion, contravenes for the other members of its Order, from their generally analogous formation, this opinion of Darwin. Doubtless, had Darwin included the primrose amongst those flowers which he experimented upon, as recorded in the volume of "Cross- and Self-Fertilization of Plants," he would have caused that flower, under the influence of the net (or greenhouse), to lose its natural virility, and would have formed the same conclusion about it as he does about the Order of the Primulaceæ generally, "that it was eminently liable to suffer from self-fertilization."

CHAPTER XII

GENERAL PREPOTENCY OF FOREIGN POLLEN IN A STATE OF NATURE IN NO WISE SUBSTANTIATED BY THE RESULTS OF DARWIN'S EXPERIMENTS

FROM the method in which Darwin conducted his experiments, he was naturally led into very exaggerated ideas about the prepotency of foreign pollen over the pollen of its own flower, whether that pollen was taken

A. From a variety ("Cr. and S. F.," pp. 393–396), or

B. From another individual of the same variety (Ib., pp. 398, 399).

A. Of the first case Darwin says, "Pollen from any other variety is often and generally prepotent over the pollen of the same flower" (p. 393).

Under this head, the first example given by him is the Yellow Mimulus (*Mimulus luteus*). This was an experiment, and therefore conducted, as in all his experiments, unless otherwise stated, under a net.[1] "The pollen of *Mimulus luteus*," Darwin says, "regularly falls upon the stigma of its own flower, for the plant is highly fertile when insects are excluded. Now several flowers on a remarkably constant whitish variety were fertilized, without having

[1] We are told, when the plants experimented upon are left uncovered (pp. 394, 397), or when pollen used for crossing was grown under the net (p. 152).

their anthers removed, with pollen from a yellowish variety, and of the twenty-eight seedlings thus raised, every one bore yellowish flowers, so that the pollen of the yellow variety completely overwhelmed that of the mother-plant" ("Cr. and S. F.," p. 394). A similar result, though in an inferior degree, followed on the same method of experimenting with *Iberis umbellata.* In this latter case, "30 seedlings raised from flowers which had not their anthers removed, of a crimson variety, crossed with pollen from a pink variety, 24 bore pink flowers, like those of the male or pollen-bearing plant" (p. 394).

We have already alluded in a previous chapter (Chap. X.) to cases in which, through some natural or accidental cause, foreign pollen would act most beneficially upon flowers, and especially upon flowers whose own pollen had been, like the flowers, from the seeds of which Darwin grew his seedlings in these instances, debarred, by the surroundings under which they grew, from reaching perfect maturity. Such was the case with these experiments *under the net* with *Mimulus* and *Iberis.* Such cases are no proof of any ordinary prepotency of foreign pollen in the fields. They merely substantiate the superior efficacy of naturally grown pollen over that which had been developed under a net.

The other examples given by Darwin in favour of the prepotency of pollen from a variety over that of its own flower do not require any explicit notice or detailed criticism, as his experiments were with ordinary garden vegetables, as the varieties of the Common Cabbage, the Raddish (*Rhaphanus satious*), and the globe and Spanish Onion (p. 395).

No experiments with *varieties of cultivated* vegetables could substantiate any theory as to the usual amount, or effect, of intercrossing of wild plants, as the reproductive organs of such cultivated vegetables are known to be exceedingly differentiated from their wild originals; they

have lost the *constancy* of wild plants and have become very variable from cultivation.[1]

Nor do Darwin's experiments with radishes and onions afford any more reliable indication of prepotency than that of cabbages. They are equally inconstant with the cabbages when put into comparison with wild plants. "There are many plants," Darwin tells us, "with stamens and pistils, which are not in any way constructed to favour cross-fertilization, but which, nevertheless, freely commingle, as cabbages, radishes, and onions, as I know from having experimented upon them."

"Animals and Plants under Domestication," vol. ii., p. 68.

The same tendency is found under cultivation in garden flowers, as varieties of the tulip, raspberry, orange, and rhododendron, etc., on which Darwin does not seem to have experimented, but merely says in reference to them that "a similar result is known to follow with the varieties of such plants" as those which he obtained from garden vegetables.

B. The second case is the prepotency of pollen of a different individual of the *same* variety over the pollen of its own flower.

Of this case Darwin says: "Scarcely any result from my experiments has surprised me so much as this of the prepotency of pollen from a distinct individual over each plant's own pollen, as proved by the greater constitutional vigour of the crossed seedlings" ("Cr. and S. F.," p. 399); and again, "a much more remarkable fact than the prepotent power of pollen from a distinct variety over a plant's own pollen is the fact that pollen from another individual of the same variety is prepotent over a plant's own pollen,

Ib., vol. i., pp. 341–343.

[1] Darwin, writing of the Cabbage, says, "Every one knows how greatly the various kinds of Cabbage differ in appearance. It would be useless to give a classified description of the numerous races, subraces, and varieties of the cabbage. The plants raised by me were not nearly so constant in character as any common kind of cabbage."

as shown by the superiority of the seedlings raised from a cross of this kind over seedlings from self-fertilized flowers" (Ib., p. 398).

Darwin, in support of his views in this case, merely instances cases where "the cross-fertilized seedlings were greatly superior in height, weight, and fertility to the self-fertilized offspring" (p. 398). These cases need no further discussion, as they have already been discussed in a previous chapter where the results which he obtained have been shown to have arisen from "the disadvantageous conditions to which the flowers were subjected, from whose seeds the self-fertilized seedlings were produced."

There are only two other cases given by Darwin in reference to prepotency which need our consideration. Darwin was anxious to ascertain "after how long a time pollen from a distinct variety would obliterate more or less completely the action of a plant's own pollen" ("Cr. and S. F.," p. 397). Two trials only, as we have stated, were made.

One, a variety of cabbage called "Ragged Jack" was crossed, uncovered, by another variety, "The Early Barnes Cabbage." The ragged Jack was first fertilized with its own pollen, and twenty-four hours afterwards by the pollen of the Barnes variety. Out of 15 seedlings raised from the seeds of ragged Jack, only 3 were mongrelized, though Darwin says that the remaining 12 plants "grew much more vigorously than the self-fertilized seedlings" (p. 397). This cannot be considered a very significant result, when the plant, though after an interval of twenty-four hours, had the selection between two kinds of pollen, and yet only produced 3 mongrels as the result, especially as Darwin says (as quoted in the note above) that his cabbages were "more than ordinarily variable."

The other experiment is one which we desire more particularly to notice, as it is more than once referred to by

Darwin as a special illustration of the prepotency of foreign pollen over that of its own flower.

"There can hardly be a doubt," Darwin says, "that with heterostyled, dimorphic plants, pollen from the other form will obliterate pollen from the same form, even though this has been placed on the stigma a considerable time before" ("F. Fl.," p. 31).

"To test this belief," Darwin says, "I placed on several stigmas of a long-styled cowslip plenty of pollen from the same plant,[1] and, after twenty-four hours, added some from a short-styled, dark polyanthus, which is a variety of the cowslip. From the flowers thus treated 30 seedlings were raised, and all these without exception bore reddish flowers; so that the effect of the pollen from the same form, though placed on the flowers twenty-four hours previously, was quite destroyed by the pollen from a plant belonging to the other form." This was a *test* case, an experiment, and therefore as usual in Darwin's experiments with the flower experimented upon under a net. How long so placed we are not informed, but it must necessarily have been for some time, and before the flowers opened, so as to prevent all risk of other cross-fertilization. Pollen from the *same* plant under the net was used for the self-fertilization of this long-styled cowslip, and so in all probability was imperfectly matured. When the *naturally grown* pollen of the dark polyanthus was used, the result became merely the "prepotency" of pollen grown unshaded over that which had been grown under a close-meshed net. Yet even from this experiment Darwin concludes, as quoted above, that

[1] This experiment is twice recorded again in "Cr. and S. F.," p. 397, and "F. Fl.," p. 241. In the repetition of this case in "F. Fl.," p. 241, there is the slight error of "another" plant for "same" plant. But "same" plant is recorded in both the other accounts, and especially in "F. Fl.," p. 31, when the reference is special to the subject.

"there can hardly be a doubt that with heterostyled dimorphic plants, pollen from the other form, will obliterate the effects of pollen from the same form."[1]

From all the above instances we consider that Darwin had no substantial grounds for his conclusion when he says, "From the various facts now given, we may conclude that pollen brought from a distinct plant will generally prevent the action of pollen from the same flower; and thus the intercrossing of plants in a state of nature will be greatly favoured and ensured" ("Cr. and S. F.," pp. 2, 399, 400).[2]

[1] The results of this very unreliable experiment are recorded as valid and established in "Origin of Species," p. 237.

[2] The Editor of the *Garden*, when introducing a paper of Mr. Meehan's into his columns, in which Mr. Meehan questioned the aid attributed to insects in fertilization—quotations from which we shall meet with below—says, "We are pleased to notice that Mr. Meehan has given expression to what we fancy many cultivators already feel, that a great deal too much has been claimed for the work of insects in plant fertilization" (vol. x., p. 493).

CHAPTER XIII

THE SO-CALLED DICHOGAMOUS PLANTS

SINCE the days of Darwin, and from the conclusions which he arrived at from his method of experimenting so that he classed flowers as "sterile," or "partially sterile," with their own pollen which did not produce seeds, or only gave imperfect results, under his net, it has followed, as his net was a great manufactory of self-sterility, that there has arisen a very exaggerated opinion as to the extent and necessity of cross-fertilization amongst flowers. It has been assumed in a multitude of cases in which there is no validity for such an assumption.

"*Nat. Sci. Rev.*," vol. iii. New Series.

Professor G. Henslow says, "Darwin's works have gone far to strengthen the belief that intercrossing is absolutely necessary for plants, and that, without it, plants tend to degenerate, and thence to ultimate extinction. This I believe to be absolutely false."

There are three methods especially (exclusive of heterostylism, which has already been examined in the dimorphic flowers of the primrose, and which will be further examined in the trimorphic form of the Purple Loosestrife, *Lythrum salicaria*), by which we are told, generally by Darwin, that cross-fertilization is favoured ("Cr. and S. F.," p. 383; by Mr. Wallace, that cross-fertilization "is secured" ("Darwinism," p. 311); and by Lord Avebury, that "self-fertilization is prevented" ("Fl. and Ins.," pp. 28, 29).

These three methods, as summarised by Mr. Wallace,

with which Lord Avebury's summary closely coincides (pp. 28–33) are—

1. By dichogamy, as in *Arum maculatum.*

2. By the flower being self-sterile with its own pollen, as in the *Crimson Flax.*

3. By the relative position of the stamens and pistils, as in *Malva sylvestris.*

Mr. Wallace gives a fourth case when the plants are diæcious. This case, and the case of monæcious plants, needs no discussion, as the natural arrangements of the stamens and pistils in the flowers obviously necessitate that the flowers should be fertilized, either by the action of the wind, or by insects, and they consequently do not come under the usual meaning attached to cross-fertilization at all.

1. The first case, in which Mr. Wallace says that cross-fertilization is secured, is by *dichogamy.*

The word dichogamous is used to express the idea that in some flowers the stamens and pistils do not arrive at maturity at the same time, and consequently that, in such cases, there can be no self-fertilization of such flowers. Lord Avebury's definition is, "though the stamens and pistils are both situated in one flower, they are not mature at the same time, and their pollen *therefore cannot fertilize the stigma.* These plants are called *dichogamous.*" Lord Avebury continues, "Sometimes, as in the Arum, the pistil matures before the anthers, and these plants are called *proterogynous;* but much more frequently the anthers mature before the pistil, and such flowers are called *proterandrous*" ("Fl. and Ins.," p. 22. The italics are ours).

Dichogamy is thus divided into two classes—proterogynous and proterandrous.

If these terms were limited in signification to the mere appearance of the one before the other—the pistils before

the stamens, or *vice versâ*—and did not exclude the fact of their ultimate concurrent maturity, there could be no disputing the applicability of such terms, both as to the *proterogynous* and the *proterandrous* conditions of some flowers—the appearance in the former case (proterogynous) of the stigmas before the anthers, and in the latter case (proterandrous) of the anthers before the stigmas. Then, in such cases of dichogamy, the precedence would be only one in appearance, not one in effect, as far as, in most cases, the possibility of the self-fertilization of the flower was concerned. But if the term "dichogamous" is not so limited, but means that all flowers to which that term—in its two divisions of proterogynous and proterandrous—is applied are incapable of self-fertilization, then, in the majority of cases, if not in all, the truth of such a statement would be very difficult absolutely to substantiate.

Darwin says that with "dichogamous plants it is not very easy, without much care, to perceive whether the stigmas are ready to be fertilized when the anthers open" ("Cr. and S. F.," p. 23). In cleistogamic flowers, which are so productive, "the pistil," Darwin says, "is much reduced in size with the stigma, in some cases hardly at all developed" ("F. Fl.," p. 310). Darwin also says, "if the pollen should fall on the stigma when it was immature, it would generally remain there till the stigma was mature" ("Cr. and S. F.," p. 23). And again, "with some species, the pistil continues growing for a long time" ("F. Fl.," p. 3).[1]

[1] A remarkable example of the stigma growing for a long time is seen in the Travellers' Joy (*Clematis vitalba*), in which "the styles are persistent, and grow out into long, feathery awns" (Bentham's "English Flora"), the Old Man's Beard of the country-people. It is met with in the order of *Compositæ*, as well as in the order of the *Umbelliferæ*; in the *Malvaceæ*, as the Common and Dwarf Mallows (*Malva sylvestris* and *M. rotundifolia*); in the Spindle Tree (*Enonymus Europæus*), ("F. Fl.," p. 289); in *Gillia aggregata* ("F. Fl.," p. 118), and in other flowers.

It is obvious, from the extracts from Darwin given above, that it is almost impossible to tell when a flower is proterandrous, as at every stage the stigma, long before it has attained its final growth, may, for the purpose of its fertilization, be perfectly mature. To make an absolute decision in such cases against the self-fertilizing power of a flower is almost impossible.

We shall examine two examples of flowers which are given as *proterogynous* in the sense as given above, of Lord Avebury's definition, (*a*) the *Arum maculatum*—the Cuckoo Pint, Wake Robin, Lords and Ladies of our hedgerows; and (*b*) members of the order *Plantagineæ*—our English plantains—which are, by appearance, the most markedly proterogynous flowers of our English flora. In examining the *proterandrous* condition, we shall also take two examples, (*a*) the Common Parsley (*Apium petroselinum*) and (*b*) the Common Monkshood (*Aconitum napellus*), as they are instanced by Darwin as examples of the proterandrous condition. In the case of all these flowers, the necessity of cross-fertilization is, by the above writers, assumed.

A. Arum maculatum.

This plant Darwin alludes to, but he never says explicitly that it is a dichogamous plant, nor that it is an instance of a purely cross-fertilized flower. It might be implied from his words, but it is not, as far as we have observed, directly expressed. He tells us that he saw several minute flies, which had pollen upon them, pass from one arum to another, and that, when he examined the arum to which they flew, he found some grains of

pollen at the bottom of the spathe, though the pollen cells of the same flower were not burst. "In another flower," Darwin says, "little flies were crawling about, and I saw them leave pollen on the stigmas" ("Cr. and S. F.," pp. 420, 421).

Mr. Wallace cites the Arum as an example of his first method (method one, above), "by which cross-fertilization is secured" ("Darwinism," p. 310).

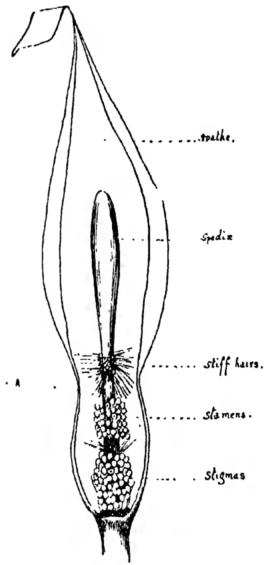

Fig. 3.—Arum maculatum; with the front portion of the spathe removed from the point marked A downwards.

Lord Avebury tells us that "the stigmas of the Arum mature before the anthers (proterogynous), and by the time the pollen is shed, *they have become incapable of fertilization. It is impossible, therefore, that the plant should fertilize itself*" ("Fl. and Ins." p. 33. The italics are ours).[1]

Now, such a statement as the above is most obviously contradicted by the Arum itself. We know of no flower which gives clearer evidence of its own self-fertilization than the Arum. We carefully examined in one year over two hundred of the flowers after the spathe had opened, and an almost equal number in a subsequent year. We never found the stigmas in *any single instance* showing any sign of becoming brownish or discoloured before the anther cells

[1] To the same effect is H. Müller's statement concerning this plant ("Fert. of Fl.," p. 562).

above them had burst; until the anther cells above them burst, the stigmas were always fresh, green, and moist. This shows distinctly that the stigmas are not past their maturity when the pollen is shed. When the anther cells burst, which they do almost simultaneously, their cases strongly contract—occupying, after bursting, only half the space which they occupied previously—and by so doing they force the pollen out, which then falls upon the slightly projecting stigmas below. The pollen is shed in so large a quantity that it covers in many cases the stigmas by which it is caught with a coating of pollen. The overplus, which is frequently considerable, falls into the bottom of the spathe. The second or third day after it has fallen, the tips of the stigmas begin to turn into a brownish hue, and to become discoloured, a sign that the stigmas are fertilized ("Cr. and S. F.," p. 343). Yet Lord Avebury tells us that "it is impossible that the plant should fertilize itself." The above facts are conspicuously patent to any observer. Yet though so conspicuous, we are told by Lord Avebury that the stigmas are "fertilized by insects." In Lord Avebury's words, "Small insects enter the tube while the stigmas are mature, and find themselves imprisoned by a fringe of hairs, which, while permitting their entrance, prevent their returning. After a while, however, the period of maturity of the stigmas is over, and each secretes a drop of honey, thus repaying the insect for their captivity. The anthers then ripen and shed their pollen, which falls on and adheres to the insects. Then the hairs at the entrance of the spathe gradually shrivel up and set the insects free, which carry the pollen with them, so that those which then visit another plant can hardly fail to deposit some of it on the stigmas" ("Fl. and Ins.," p. 32). Compare Müller, p. 562.

In this description, the fringe of hairs on the spadix seems to exist there, in order to imprison the flies till the pollen has fallen; the anthers seem to burst that the pollen

may fall upon the flies; the stigmas are made to give out honey *after their maturity is passed, and when they have begun to wither*, to keep the flies alive for their next move, and to reward them for their forced imprisonment. After all their imprisonment and reward, the uncertainty still remains whether they will, after their escape, choose to go to another Arum or not; and the still further uncertainty whether they may not fail—"can hardly fail"—to deposit some of the pollen on the stigmas. Such a fanciful, not to say, clumsy, interrelation of flies, anthers, and stigmas, for the fertilization of these flowers, can scarcely be saddled with any justice upon Nature.[1]

About the forced imprisonment of small flies, Darwin says, "this statement has been shown by Hildebrand to be erroneous," and Darwin proves that it is incorrect, and that the small flies can escape before the hairs above wither, by his own experiment ("Cr. and S. F.," p. 420).

If it were correct that flies were the necessary agents for the fertilization of these flowers, but few comparatively would be fertilized. Out of the large number of opened spathes that we gathered, flies were found in about one in every eight or ten spathes, and *most of these were dead.* Darwin says of the flies which he saw in the spathes, "many of these insects were lying dead at the bottom" ("Cr. and S. F.," p. 420). Sometimes a considerable number of these small flies—flies about a quarter the size of our common house-flies—we found dead, mixed with a few living ones.[2] The average usually of dead and living ones in a spathe, when found, is from two to ten. On one occasion we found

[1] H. Müller attributes to the stupidity of flies the production of such a condition in Arum. "The stupidity of flies also favoured the production of certain contrivances to insure crossing as the prison flowers of Arum"! ("Fert. of Fl.," p. 594).

[2] We sent two or three specimens of the flies we found to the authorities of the Insect Department of the Natural History Museum, and Mr. R. J. Pocock replied, "the flies are a species of *Pericoma.*"

about twenty, of which only five were alive. A few slightly larger flies are also found about half the size of our house-fly; these were sometimes dead, sometimes alive. Even if all these small flies had been alive and had escaped—if 50 or 100 flies had escaped—and if they had all chosen to visit next another Arum, it would have been quite impossible for them, considering the very small amount which such small flies would have carried, to load the stigmas of another plant with a sufficiency of pollen to fertilize all the stigmas. Many vacancies would have assuredly been seen in the matured clusters; whereas, when the fruit is set and appears uncovered in the autumn, the red berries are closely packed together on the spadix. Moreover, we have never seen any pollen on the stigmas of the plants we gathered unless the anther cells of their own flower were burst. After the bursting of the anthers, the stigmas are absolutely coated with pollen.

The spathes are occasionally occupied with a small spider, which twists its web round the anther cells, or stigmas, or both. We found these webs in about one in every twelve flowers. In thirteen flowers, we caught the spiders themselves, which were very small ones, but quite large enough to account for the dead flies at the bottom of the spathes. One of these spiders was a small red one, the others were usually of a greenish brown hue. The existence of these small spiders seems to have been overlooked, and the death of the flies attributed to their imprisonment alone.[1]

Another very probable reason exists for the dead flies at the bottom of the spathes, viz. their feeding on the intensely

[1] We sent three of the spiders to the authorities of the Insect Department of the Natural History Museum, and Mr. R. J. Pocock replied, "One of the spiders is too young for identification, but belongs to the genus *Thesidium*, in all probability; the two other, Arachnida, are young specimens of *Chibiona holosericea*."

acrid juice which, as is well known, is secreted by the tissues of the flower, which they would obtain from the open surfaces of the stigmas, and which would probably act upon them with poisonous results.

The Arum, in face of the circumstances mentioned above, though apparently proterogynous, cannot be a proterogynous plant in which cross-fertilization is "secured," and self-fertilization is "prevented." It is a purely self-fertilized flower.

B.—Plantain Family.

Some of the Plantain family (*Plantagineæ*) are, as we have said, the most remarkably proterogynous-looking flowers of our English flora. Lord Avebury designates the three species *P. major*, *media*, and *lanceolata* all as proterogynous. So they would appear to any casual observer. Careful observation of the flowers of the two first-mentioned species will show this to be incorrect, for though the stigmas in both species appear before the anthers, and whilst the anthers still remain in their corolla, yet the stigmas do not pass their mature condition until in each case the anthers in the same flowers are mature as well. This can be seen very plainly in *P. major*, and *P. media*, and markedly in *P. maritima*. These flowers should be examined at their earliest appearance, when only two, or three, or four rows of flowers are out upon a spike. So far from the flowers of these species being proterogynous in Lord Avebury's definition of the term, we have frequently seen the stigmas of the lowest row of flowers on the spike perfectly fresh and green, even at their tips, when not only the anthers of their own flower are perfectly extruded and ripe, but when the anthers of four to six rows of flowers above them are also extended and mature. We have seen in *P. major* seven rows of stigmas perfectly fresh, with their anthers unfolded—

one above another. Even H. Müller says of *P. media*, "the stigmas are always fresh after the anthers have shed their pollen." *P. maritima* is even a stronger witness against protogymy. Mr. A. W. Bennett says that "in *P. media* and *P. maritima* the stigma rather lags behind the stamens than otherwise." "Fert. of Fl.," p. 508. *Journal of Botany*, vol. viii.

Definite observation of *P. lanceolata* is more difficult, because the spike is much shorter and the flowers are more closely packed. It requires to be examined at its first appearance in spring. If a spike is gathered which has extruded the lowest row of stamens only, and has no other flowers so advanced in close proximity, it will be found, as we have frequently observed at such early season, that the stigmas are perfectly fresh and without any discoloration in the same flower in which the stamens are ripe and discharging their pollen. When the flower is more advanced, or the season even is more advanced, it is difficult to find a flower so isolated as to give a true interpretation of its natural condition when surrounded with other flowers of the species, the stigmas on the spikes of *P. lanceolata* are generally fertilized, and become withered and discoloured by cross-fertilization from adjoining flowers before the anthers of their own flowers are exserted.

In all the Plantagineæ, the stigma and stamens are developed on the spike from below upwards, and the stamens are provided with unusually long, erect, and flexible filaments. The pollen of the ripe anthers, consequently, not only falls upon the stigmas of their own flowers, but the anthers are beaten against the stigmas of the rows above them, or the pollen from neighbouring flowers is carried to them by the wind. In such cases the stigmas above will become fertilized and so discoloured before the anthers of their own flower are extruded. This is more particularly seen, as we have said, in *P. lanceolata*, and has given real cause in very many cases for its being considered a

proterogynous flower. They consequently are proterogynous in the sense that the stigmas precede the anthers in arriving at maturity, but if the stigmas are not fertilized by the anthers of other flowers, they remain perfectly fresh until those in their own flower are developed. The members of the Plantagineæ are not proterogynous in the sense that in them cross-fertilization is "secured," or self-fertilization is "prevented."[1]

A.—Wild Parsley (*Apium petroselinum*).

The Common Parsley (*Apium petroselinum*), a member of the Order of the Umbelliferæ, is enumerated among *proterandrous plants*. "The Umbelliferæ," Darwin says, "are proterandrous, and can hardly fail to be cross-fertilized by many flies and small Hymenoptera which visit the flowers" ("Cr. and S. F.," p. 172). We give the Common Parsley as an example of the Order of Umbelliferæ, as it is the only member of this order that Darwin experimented upon.

A plant was covered with the net, and "it apparently," Darwin says, "produced as many and as fine spontaneously

[1] We have never seen a bee visiting any of the *Plantagineæ*. It must be, in England, a most rare and exceptional case, and so bees could have no influence in any cross-fertilization; nor can we remember to have seen any insect upon the spikes collecting pollen. These flowers are to be met with almost on every roadside (excluding *maritima*), and therefore can be by every one constantly observed.

H. Müller tells us that the hive-bee (*Apis mellifica*) visits a certain variety in Germany of *P. lanceolata* and *P. media* for the sake of the pollen. The very long and freely motile filaments, and the quivering of the anthers of the plantains would render such collection of pollen extremely difficult. H. Müller gives us a singular method by which the bee overcomes the difficulty. "The honey-bee flies buzzing to a spike, and while it hovers in the air it spits a little honey on the exserted anthers"! (p. 505). To see a bee spit when hovering would require a power of eyesight which few could claim to possess.

self-fertilized seeds or fruits as the adjoining uncovered plants." These flowers under the net must, in accordance with Darwin's statement, have been almost *unexceptionally self-fertilized.* Insects were excluded, and "when they are excluded, the wind does hardly anything in conveying pollen" ("F. Fl.," p. 93).

The seedlings also raised from the seeds of this covered plant equalled those of the crossed plants outside the net, even after their most vitalized seedlings had been thrown away. "Some of the two lots of seeds were left on sand," Darwin says, "but nearly all the self-fertilized seeds germinated before the others, so that I was obliged to throw them away."[1]

When the remaining seedlings of the two sets were finally compared "neither side had any substantial advantage over the other." Yet this plant and the entire order of the *Umbelliferæ* to which it belongs is classed by Darwin as *proterandrous.* This case, as far as it goes, shows that the condition of this Order is only apparently, not really, proterandrous. Yet in contrast to the results here obtained by Darwin, H. Müller, when speaking of the Field Eringo (*Eryngium campestre*), says, "in this cross-fertilization, as in *all other* Umbellifers, *can alone* take place."[2] "Fert. of Fl.," p. 227. (The italics are ours.)

[1] Darwin, in his experiments with seedlings, in order to compare the growth of plants raised from self-fertilized seeds with those raised from cross-fertilized ones, planted the seeds on the opposite sides of flower-pots, but if any of one set came up before any of the other set appeared, these were thrown away until some on both sides of the pot appeared.

[2] The Umbelliferæ are very deceptive. There are often very many flowers, especially those which are upon the exterior rays, which are perfectly infertile, and which never produce any fertile capsule. In such infertile capsules, *the stigmas often never appear at all.* We have gathered umbels in which three or four capsules only are fully developed, and on the same umbel twenty to thirty rudimentary capsules which *produce no stigmas* nor fertile fruit. In the early stages of such flowers, a hasty observer would naturally

B.—COMMON MONKSHOOD (*Aconitum Napellus*).

A similar instance of the fallacy of judging by appearance occurs in the Common Aconite (*Aconitum napellus*), a flower which Darwin, after Spengel, says is "strongly proterandrous."

It is cited by Darwin more immediately to show that a white variety of the flowers, which had their corollas bitten through, and so were not cross-fertilized, are inferior in fertility to those of a blue variety of the same flower, which were not so bitten through. "Dr. Ogle," Darwin says, "gathered a hundred flower-stems of the common blue variety of the Monkshood (*Aconitum napellus*), and not a single flower was perforated; he then gathered a hundred stems of a white variety growing close by, and every one of the open flowers had been perforated. This surprising difference in the state of the flowers may be attributed, with much probability, to the *blue variety being distasteful to the bees*, from the presence of acrid matter which is so general in the *Ranunculaceæ*, and to its absence in the white variety in correlation with the loss of the blue

decide that the plant was proterandrous, from the appearance of anthers and no stigmas. In the Hemlock Œnanthe (*Œnanthe crocata*), it is very noticeable that in the central flowers of the umbels the stigmas are often developed whilst the anthers in the same flower have not become erect and are unburst. These flowers, if appearance were to decide, would be called proterogynous. In other flowers on the same head the stigmas are scarcely more than perceptible when the anthers are erect, and have almost parted with their pollen. These, from their appearance, might be called proterandrous. Other members of the order present very similar features. In the Common Fennel (*Fæniculum vulgare*), the pistil and stigma, when the pollen is ripe, are scarcely more than small round dots just raised above the general surface of the capsule, and even when the fruit is ripe the stigmas are usually but little extended. Yet Darwin's experiments on Apium showed that this order was self-fertilizing.

tint. According to Sprengel, this plant is *strongly proterandrous;* it would, therefore, be more or less sterile unless bees carried pollen from the younger to the older flowers. Consequently the white variety, the flowers of which were always bitten instead of being properly entered by the bees, would fail to yield the full number of seeds, and would be a comparatively rare plant, as Dr. Ogle informs me was the case" ("Cr. and S. F.," p. 431. The italics are ours).

On the other hand, the blue variety, on account of "its acrid matter so common to the *Ranunculaceæ,*" would not be visited at all by the bees on account of the "acrid juices being distasteful to them." The two flowers stood accordingly on the same footing as to cross-fertilization, and some other cause than the boring of the white variety by the bees—as perhaps the chemical constitution of the soil—must have brought about the greater number of the blue than of the white variety. It shows that the flowers were only proterandrous in appearance, not in reality. If otherwise, as neither of them was cross-fertilized, each would have been liable to absolute extinction.

The case of the Arum, where the pistil seems to precede the anthers in maturity, when in reality, for the fertilization of its flowers, such is not the case; and the case of the Common Parsley (*A. petroselinum*) where the anthers seem to precede the stigmas in maturity, which is also shown—in respect to the fertilization of the flowers—by Darwin's experiment not to be the case, should make observers cautious as to concluding, from the mere appearance of the stamens or pistils, that the one precedes the other as to its period of maturity, to such an extent of dichogamy "that the pollen cannot fertilize the stigma." [1]

[1] We are not ourselves aware of any wild English plant being in such a condition. Darwin cites *Lobelia fulgens* as being in that condition, and says that it was so "strongly proterandrous" that the "pollen was mature, and shed long before the stigma was mature." He

No plant, if Lord Avebury's definition of dichogamy is accepted, should be called *proterogynous* unless the stigmas have begun to turn brown or discoloured before the anthers of the same flower have opened; nor should any plant be called *proterandrous* unless, when the anthers have discharged their pollen, the stigmas of the same flower have not appeared. When the terms are applied otherwise, they become misleading and incorrect.

consequently gathered and kept the pollen till the stigma was sufficiently advanced ("Cr. and S. F.," p. 179). But this was a foreign cultivated garden or greenhouse plant, and was "kept in a greenhouse." Any anomalous condition may, as it is well known, be produced by cultivation. Another foreign cultivated plant, *Dianthus caryophyllus*, was "so strongly proterandrous," that Darwin thought that when plants of it "spontaneously fertilized themselves under the net," and produced an abundance of seeds, that the plants "had varied so as to mature their pollen and stigmas more nearly at the same time than is proper to the species"! (Ib., 135, *n.*).

CHAPTER XIV

UNNATURAL CONCLUSIONS DRAWN FROM THE RESULTS PRODUCED IN FLOWERS PLACED UNDER UNNATURAL CONDITIONS

A. "Their own pollen being to their own flower as so much inorganic dust."

1. Perennial Flax (*Linum perenne*).
2. Crimson Flax (*L. grandiflorum*).

B. "Their own pollen to their own flowers acting as poison."—*Certain Orchids.*

A.—1. Perennial Flax (*Linum perenne*).

Darwin, under the influence of the net, brings a heavy charge against the arrangements of Nature. "A good observer (H. Lecoq)," Darwin tells us, "states that in *Linum Austriacum* (which is a heterostyled plant, and is considered by Planchon as a variety of *Linum perenne*), the anthers open in the evening before the expansion of the flowers, and that the stigmas then are almost always fertilized. Now, we know positively that, so far from *Linum perenne* being fertilized by its own pollen in the bud, *its own pollen is as powerless on its stigma as so much inorganic dust*" ("F. Fl.," p. 98. The italics are ours).

This very positive assertion of Darwin's does not accord with his own experiments recorded on a preceding page ("F. Fl.," p. 92). In those experiments, the flowers of 13 short-styled plants of *Linum perenne* under the net *which*

were not fertilized, produced 12 capsules, and each capsule on an average 5 to 6 seeds (10 seeds being the maximum produced by each flower). Now, Darwin tries to account for this produce—as some capsules were very fine, and as 5 were borne upon the same twig—by saying, "I suspect that some minute insect must have accidentally got under the net, and brought pollen from the other form" (which was also under the net) "to the flowers which had produced this little group of capsules." But we know by Darwin's own statements that the meshes of the net were so fine that nothing larger "than the minute Thrips" could get into the net, and that this is so minute an insect that, as Darwin assures us, "a cross of this kind (from a Thrips) does not produce any effect, or at most only a slight one." Yet "some of these apsules" on *Linum perenne* "were very fine capsules." Nor could the wind, by Darwin's own confession, have effected cross-fertilization in this case. On an immediately succeeding page ("F. Fl.," p. 93) Darwin says, in reference to these very experiments on *Linum perenne*, "the wind does hardly anything in the way of carrying pollen from plant to plant when the proper insects are excluded."[1]

So, under all these disadvantageous conditions—of a close-meshed net; of the minimizing of the solar rays; of the deprivation of the influence of the wind, and consequently

[1] Darwin gives, in the succeeding passage to the above, a very curious reproof to botanists who attribute more influence to the wind than to insect-fertilization; a reproof based on the insufficiency of the wind in producing fertilization, when the plants are thus surrounded and itself almost excluded by an insect-excluding net. He says, "I allude to this fact because botanists, in speaking of the fertilization of various flowers, often refer to the wind or to insects as if the alternative were indifferent. According to my view, this idea is entirely erroneous" ("F. Fl.," p. 93). The two cases—the influence of the wind under a net, and its influence in the open fields—are not in any way parallel. The reproof, consequently, is very inapplicable.

of any adequate shaking of the flowers;—these 13 short-styled plants still produced 12 capsules, and amongst them "some very fine capsules," and on the average the capsules contained 5 to 6 seeds each. In fact, as far as the capsules go, the product of these capsules on the 13 short-styled plants compares very favourably with the product of the capsules of the 12 short-styled flowers on the same plants *fertilized by long-styled pollen*, and consequently by their being fertilized not labouring under equally disadvantageous conditions. These latter 12 flowers did not produce more than 8 good capsules, containing on an average 8 good seeds each. Thus, on the same plants, 12 short-styled flowers cross-fertilized produced altogether 64 seeds, whilst the 13 flowers unfertilized artificially produced 66 seeds. Nor can we accept the suspicion of Darwin, "that some minute insect" had got under the net, and had fertilized these flowers from the other form. We have already given above the reasons which militate against such a supposition. Some of the capsules were very fine, and therefore the flowers must have been well fertilized. It would consequently have required very many minute insects, or very many journeys of one such minute insect, to have accomplished this. The Thrips, as we have already seen, does not usually pass from plant to plant. Also it would have been very peculiar indeed, if there were several minute insects under the net, that all the insects should have fixed on the same twig, or that a single minute insect should have done the same, and should have passed from plant to plant, and carried accidentally, by many journeys to and fro, such an amount of pollen or such an equal portion to each flower as is here necessarily supposed. This supposition of Darwin seems to us to have no other basis whatever than his own idea as to these flowers, "that it is absolutely necessary, as we know, that insects should carry pollen from the flowers of one form reciprocally to those of the other" ("F. Fl.," p. 95).

This is a marked instance (and there are many other instances) in which Darwin allows his own subjective prepossessions to override objective facts.

Darwin tells us that Hildebrand confirms his results: that Hildebrand "*placed in his house* a short-styled plant, and fertilized 20 flowers with their own pollen," and that "these flowers did not set a single capsule" ("F. Fl.," p. 92. The italics are ours). But we shall see below (Chap. XVIII.) the sterilizing effect of Hildebrand's method —a method much more sterilizing than Darwin's net. It is on this experiment of Hildebrand's, apparently, that Darwin seems to have founded this positive assertion that the pollen of *Linum perenne* had no influence on its own stigma, as no other experiment than his own (in which the flowers were —under the conditions in which they were placed—more than measurably productive with their own pollen), and those of Hildebrand, are alluded to in the context concerning this Linum.

Darwin, too, himself confesses their own self-fertility. "We have reason to believe," Darwin says, "that short-styled plants of *Linum perenne* are in a slight degree more fertile with their own pollen than the long-styled plants" ("F. Fl.," p. 92).

We cannot see how Darwin, after such a statement of his own experience, and such a record of their own fertility even under the net, as that which we have given above, had any ground whatever for his positive assertion that "the pollen of *Linum perenne* had no more power on its own stigma than so much inorganic dust." [1]

[1] A particular instance of the injurious effect of the net on natural fertility is seen in reference to these experiments with *Linum perenne*. The 13 short-styled plants under the net to which we have referred, and which had their branches interlocked with those of 11 long-styled ones, together yielded 12 good capsules; whereas *one* short-styled plant, growing just outside the net and close to a long-styled plant, also yielded 12 capsules. Thus 13 short-styled plants inside the net,

2. The Crimson Flax (*Linum grandiflorum*).

The very same statement is made by Darwin concerning the long-styled form of the Crimson Flax (*Linum grandiflorum*) which he makes concerning the perennial flax. "In the long-styled form, the stamens equal the pistil in length, but their pollen has no more effect upon it than so much inorganic dust" ("F. Fl.," p. 266). *Vide* Fig. 23.

Mr. Wallace cites the case of the crimson flax—"from the flower being self-sterile with its own pollen"—as an illustration of his second mode "of securing cross-fertilization" (W. "Darwinism," p. 310). Lord Avebury also quotes this case to almost similar effect, saying, "By a series of careful and elaborate experiments, Mr. Darwin has shown that this species is almost entirely sterile with the pollen of its own form; the pollen of *L. grandiflorum* is differentiated with respect to all the flowers of the same form, to a degree corresponding with that of distinct species of the same genus, and even of species of distinct genera" ("Fl. and Ins.," p. 77).

This opinion of Darwin originated from experiments upon 11 plants in his garden, 8 of which were long-styled and 3 short-styled. Two of the long-styled "grew in a bed 100 yards off all the others, and separated from them by a screen of evergreens" ("F. Fl.," p. 83). These two plants, though they bore a great number of flowers during the summer (1861) yet produced no seed. In the autumn,

very similarly situated in reference to long-styled plants, excepting the presence of the net, were equalled in produce by 1 plant outside. Nor would the flowers of the plant, in greatest probability, have been cross-fertilized in either case to any extent, as bees or insects are scarcely known to visit this Linum. For the flowers under the net, the action of the wind and sun was in a great measure nullified; for those in the open air, their influence was fully exercised on the flowers, and so would cause their full fertilization.

Darwin cross-fertilized 12 of these flowers with the pollen of the short-styled which grew at a distance from them. The result was 6 fine capsules. Yet on this circumstance, in reference to two plants, Darwin chiefly relies for the absolute statement above, as to the infertility of these long-styled flowers with their own pollen. Such a result as the above, when the flowers were crossed, might very naturally arise from the possibly accidental healthier growth of the plants from which the short-styled pollen was taken. Such a circumstance is of very ordinary occurrence, and would be particularly likely to occur in an *exotic plant* like the *Crimson Flax*. We cannot consequently regard the failure of these long-styled flowers to produce capsules with their own pollen, as at all a decisive indication that they are self-sterile in their native habitat.[1]

On the other hand, the remaining 6 long-styled plants in the garden which were not artificially fertilized in any way, produced 14 capsules. Twelve of these were produced on a plant growing near to a short-styled one, so Darwin *suspects* that its flowers had been cross-fertilized, as he suspected it in *L. perenne*.[2] On the other plants which bore 2 capsules he makes no observation.

[1] We are not told, unfortunately, how near the two long-styled plants were placed to the screen of evergreens. In such a case, it would have been advisable that the assurance had been given that the plants were not so close to them as to have affected the maturing of their pollen by the contiguity.

[2] Yet Darwin says, in reference to two of the three short-styled flowers which he "repeatedly watched," that he only once saw a humble-bee momentarily alight on one and then fly away;" and that "they were but sparingly visited by insects" (pp. 84, 86). Moreover, the flowers, on which he saw this humble-bee, "did not stand very close to the long-styled one." It seems very improbable therefore, that any cross-fertilization should have occurred in this flower. His suspicions are very far from any verification. It is most rare and exceptional to see any bee visit our wild English linums. They are nectarless.

Again, *under the net* nearly 100 long-styled flowers fertilized by "own form" pollen, and many others self-fertilized under the net, produced 3 capsules which produced altogether 5 seeds. Darwin thinks it probable that even this produce, as short-styled flowers were also growing under the net, "resulted from their fertilization with pollen from the short-styled plants by the aid of Thrips" (p. 85).

This produce of the long-styled flowers of *L. grandiflorum*, though very meagre, is yet, putting aside Darwin's mere suspicions, substantial evidence of the self-fertility of the flowers, especially as two of the capsules came under no suspicion, and still more especially, as *L. grandiflorum* is an exotic plant, whose natural habitat is in the hot climate of Algeria. The wonder is, not that the flowers of an exotic plant set so few seeds, as that they seeded at all, particularly as Darwin tells us that "he had never heard of an instance of the *Linum flavum*"—a South-European plant—"seeding in this country" (p. 99). He confesses also "that our English climate cannot be very favourable to this North-African plant" (p. 85).

Darwin made ten other experiments as to the growth of the pollen tubes in the long-styled stigma when cross-fertilized, and when fertilized by its own pollen. As these experiments were not intended by Darwin to produce capsules, no definite conclusion as to the ultimate results can be drawn. If any ultimate results had been arrived at in these experiments, their value, in our opinion, would have been completely invalidated, as Darwin tells us that "the experiments were tried on plants grown in pots and brought successively into the *house*" (p. 87. The italics are ours).

Moreover, all the 100 flowers *under the net*, mentioned above, "were raised in a hot-bed" (p. 84). Exotic plants, transplanted from a hot-bed into the open air, and then placed under a net where the power of the sun's rays would be still further diminished than that usually experienced in

our temperate climate, can afford no reliable evidence whatever as to the self-sterility of the long-styled plant when it grows in its own natural habitat of Algeria. With the above evidence in favour of its self-fertility, and with Darwin's singular admission, "the short-styled plants"—which he allowed were self-fertile—"seem to be slightly more fertile with their own pollen than the long-styled" ("F. Fl.," p. 86)—we may consider that his statement that the pollen of the long-styled "on its own stigma is like so much inorganic dust," is distinctly unsubstantiated.

B.—UNNATURAL CONCLUSION—"THEIR OWN POLLEN TO THEIR OWN FLOWERS ACTING AS POISON"—DRAWN FROM UNNATURAL CONDITIONS.

CERTAIN ORCHIDS.

Darwin's heaviest indictment against the arrangements of Nature is that "there are extraordinary cases in which pollen from the same flower *acts on the stigma like a poison*" ("Cr. and S. F.," p. 342); in fact, cases in which Nature poisons herself. Now, we should be very slow, indeed, to believe that such a condition as this last can be found in the floral kingdom, when the flower is growing in its natural habitat and under natural conditions. The same remarks may be applied to such a supposed case, which the late eminent hymenopterist, Mr. Frederick Smith, of the British Museum, applied to a certain theory which had been formulated concerning the destruction of the larva of Andrenidæ (a family of bees) by the parasitic Nomada. "It appears," Mr. Smith says, "so contrary to all natural laws, that I cannot think the theory even probable; where a destruction of animal life is observed, it can usually be traced to some reasonable cause, as the destruction of the

larva of certain Lepidoptera being a check on their super-abundance. Smith's "British Hymenop. Acul.," pt. i., p. 23.

This may be applied, as we have said, equally to the vegetable kingdom. Darwin says that "Fritz Müller discovered that the pollen masses of some Orchids acted on their own stigma as a poison" ("Cr. and S. F.," p. 331). Lord Avebury gives a fuller account of the same. His lordship says, "Fritz Müller has recorded some species in which pollen placed on the stigma of its own flower acted on it as a poison: the flower faded and fell off; the pollen grains themselves, and the stigma in contact with them, shrivelled up, turned brown, and decayed: while other flowers on the same branch, which were not so treated, retained their freshness" ("Fl. and Ins.," pp. 7, 8).

It is difficult to give any other intelligent solution of this action of the pollen on the stigma of its own flower than that the unnatural condition in which the flowers were placed, and the unnatural manner in which the flowers were treated, produced unnatural results. The flowers were being experimented upon, as they were artificially fertilized, and so were, in all probability, under protection in a greenhouse, which was Fritz Müller's usual method, we believe, of experimenting. With such an equatorial climate as that of Brazil, where the experiments were made, and with the flowers excluded from natural atmospheric influences, unnatural results would be both more rapid and more pronounced. In such a climate a withering and shrivelling process might immediately set in when an undue call upon the activity of unhealthily grown tissue was made by an abundant application of pollen.[1] "The other flowers

[1] Such a result accords with Professor G. S. Boulger's observation: "A high state of cultivation, or any excess of food, predisposes to the degradation of organs, the excessive growth of parenchyma, rapid growth, and disease." *Nature*, vol. x., p. 520.

on the same branch retained their freshness." This would result from the flowers being protected, and so no pollen would be shaken upon them by the wind: or it would fall in such small quantity that no extensive vegetation nor accompanying withering would be caused by it. We cannot but think, therefore, that such an unnatural effect as that described arose from the unnatural conditions under which the flower was placed, and by which it was tested. It appears as contrary in the vegetable kingdom "to all natural laws" when flowers are naturally grown, as the theory alluded to above appeared to Mr. Smith in the animal kingdom. "Nature we have never observed to be so wasteful," and much less to be so poisonous to herself.

We have seen in the preceding pages the amount of partial and complete sterility which Darwin produced under his net, and attributed to Nature. He came to the conclusion that heterostyled plants required reciprocal fertilization; that other flowers were partially or completely self-sterile with their own pollen: until at last he reached the climax of differentiation between the pollen and stigma of the same flower as that attributed to *Linum perenne*, *L. grandiflorum*, and the *Brazilian Orchids*. It was doubtless from such results with his own net, and from the results found by the unnatural methods adopted by other experimenters, as we shall see below, that Darwin was led to express his surprise at the amount of "self-sterility" in the vegetable kingdom. "In considering," Darwin says, "the cases above given of complete and almost complete self-sterility, we are first struck with their wide distribution throughout the vegetable kingdom. Their number is not at present large, for *they can be discovered only by protecting plants from insects*, and then fertilizing them with pollen from another plant of the same species, and with their own pollen, and the latter must be proved to be in an efficient

state by other trials" ("Cr. and S. F.," p. 341. The italics are ours).[1]

We are here told that sterile flowers can only be discovered by using for the investigation the very means which produces the sterility.

[1] It is not sufficient for a fair trial, as Darwin suggests, that "the pollen used must be proved to be in an efficient state by other trials," unless both flowers—the flower on which the trial is made as well as the flower from which the pollen is taken—are grown under the net. If both sets are grown under the net, then the result could only show, in many cases, their relative power on the stigma "under its changed conditions of life ("Cr. and S. F.," p. 341), and not whether the plant was partially or absolutely self-sterile when growing under natural conditions.

CHAPTER XV

THE MALLOWS

The Common Mallow (*Malva sylvestris*) and the Dwarf Mallow (*M. rotundifolia*).

The third method—the relative position of the stamens and pistils—by which cross-fertilization is "secured" is exemplified, Mr. Wallace tells us, in the "Common Mallow."

There are two species of mallow which are generally met with throughout England—the Common Mallow (*M. sylvestris*) and the Dwarf Mallow (*M. rotundifolia*). These species are often found growing in the same locality. The Dwarf Mallow is, in our experience, much more rarely met with than the Common Mallow. It is also a much smaller and less conspicuous flower. It usually begins to bloom at a slightly later period, and continues in bloom much later than the Common Mallow. We have found it in mild seasons fully out in flower, even in the middle of December.

Both species resemble each other in their essential organs at their earliest stage. The stigmas in both flowers are surrounded by a pyramidal group of anthers, as seen in Fig. 4. At this stage, the stigmas are completely enclosed by the anthers and their filaments. When the stigmas begin to burst through this envelope, the anther cells also begin to burst and to part with their globules of pollen. The fertilization of both these flowers is concurrent with, or very shortly after, the appearance of the stigmas.

MALVA SYLVESTRIS.

The method by which cross-fertilization is secured in *Malva sylvestris*, as explained by Mr. Wallace, is "by the stamens and anthers being so placed that the pollen cannot fall upon the stigma, while it does fall upon a visiting insect which carries it to the stigma of another flower. This effect is produced by the motion of the stamens *which bend down out of the way of the stigmas before the pollen is ripe* (W. "Darwinism," p. 310. The italics are ours).

FIG. 4.—First stage of both *Malva sylvestris* and *Malva rotundifolia*.

FIG. 5.—Second stage of *Malva sylvestris* at its period of fertilization when stamens and stigmas are mature.

H. Müller states that "The ends of the anther filaments, before the stigmas are mature, curl outwards so far that spontaneous fertilization is impossible." "Fert. of Fl.," p. 143.

To the same effect is Lord Avebury's statement ("Fl. and Ins.," p. 46).

The figure which is given by all the above-named to illustrate the stage of the flower at which fertilization is accomplished, is that represented in Fig. 6.

At this stage cross-fertilization is supposed to take place through the agency of insects. Mr. Wallace also states that "the anthers bend down out of the way of the stigmas before the pollen is ripe."

We feel assured that every careful observer of the facts connected with these flowers will find that the suppositions above as to the method of the fertilization of the flowers are not correct. The anthers dehisce and discharge the chief portion of their pollen before they finally turn down. The flowers are plainly and conspicuously subject to self-fertilization before this final turning of the anthers is accomplished.

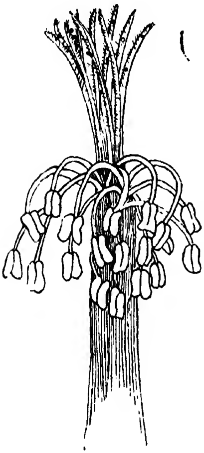

Fig. 6.—*Malva sylvestris*, or Common Mallow, in last stage after fertilization has taken place.

This may be seen if the flowers are examined at an early stage when the stigmas have issued through the enveloping anthers, and are not much extended, and whilst the upper anthers are surrounding the stigmas. After the stigmas issue from the anther covering, they begin to radiate outwards (Fig. 5). When the stigmas thus begin to radiate outwards, the anther cells are bursting, and the pollen is mature.[1] As the stigmas radiate outwards, and before the upper anthers have begun to turn definitely downwards, the stigmas may be seen dotted with the pollen globules from the anthers which surround them. Through this stage all the flowers pass. It is absolutely necessary that the observer should examine the flowers at this stage of development (Fig. 5), for at it the deposition of the pollen on the stigmas takes place. The stigmas are rough on their inside surface with stiff hairs for catching the

[1] Frequently even before the stigmas begin to radiate, the pollen granules may be seen on their tips. We have frequently at that stage seen pollen upon them. On one occasion 10 globules of pollen were on the tips of the stigmas.

pollen, and are smooth on their outside surface. The bees, in visiting the flowers at this stage, would not come in contact with the inside face of the stigmas at all. The bee's operations, as it almost invariably lands on the inside of the expanded corolla, would be conducted outside the stigmas whether in collecting pollen, or searching for honey at the base of the staminal column. They would generally at most touch the smooth, outside face of the stigmas. The wind, by shaking the flowers, transfers the pollen to the stigmas. The flowers also *habitually close in the evening*, and so press the anthers and stigmas into closer contact. The pollen globules thus brought into contact with the stiff hairs on the inner face of the stigmas are firmly held there by a glutinous kind of secretion with which they are invested.

The anthers, when they reach the position represented in Fig. 6, have parted with almost all their pollen globules, and scarcely anything is left but the anther husks. Before this position is reached, the pollen must necessarily have been mature, as it would not otherwise have been shed. The stamens consequently do not "bend down out of the way of the stigmas before the pollen is ripe," nor are they so arranged "that the flower cannot fertilize itself."

Even if ocular proof to the contrary were not at hand, we should be very slow to believe that, in a flower so framed, Nature was so wasteful in her arrangements that she would leave the production of seed to the mere chance of visiting insects, especially as in the evenings, and in dull, unpropitious, and rainy weather, the flowers of the mallows remain closed. "Nature," as Mr. Hassall says, "is seldom uselessly prodigal of her resources." *Annals of Nat. Hist.*, vol. viii.

THE DWARF MALLOW (*M. rotundifolia*).

We give here an exact representation of the position of the stigmas and anthers of *M. rotundifolia* gathered before the stigmas and anthers have begun to turn definitely downwards—Fig. 7. On the stigmas of the flower represented in Fig. 7 there were, when we gathered it, 20 pollen granules, 6 of them being on a single stigma. It is

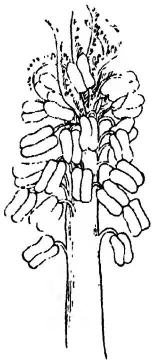

FIG. 7.—*Malva rotundifolia*, Dwarf Mallow, in second stage when pollen and stigmas are mature.

FIG. 8.—*Malva rotundifolia*, Dwarf Mallow, in last stage after its fertilization.

at this stage, as in *M. sylvestris*, and before the turning downwards of the anthers is definitely accomplished, and whilst the anthers themselves are still almost upright, that

the deposition of the pollen on the stigmas takes place. In this flower, one of the anthers which was burst with the pollen globules exposed, was actually lying in the midst of the stigmas as represented in Fig. 7. This flower was gathered in the middle of November, when all bees had long disappeared, so that it was impossible to attribute to them the carrying of the pollen which was found upon the stigmas. We have gathered in November many of the flowers with the pollen globules similarly deposited upon the stigmas, whilst many of the stamens were still in an upright position.

After the pollen has been deposited upon the stigmas and the stigmas fertilized, the latter continue to grow (as in many other flowers) and to decline, so that at last they reach the position as represented in Fig. 8. In this position the stigmas lie intermixed with the anthers. At this last stage (Fig. 8), H. Müller represents "*Malva rotundifolia* as in the act of fertilization." Lord Avebury represents by a similar figure the period and method of the self-fertilization of the flower, saying, "In *Malva rotundifolia* the stigmas are elongated, and twine themselves among the stamens so that the flower can hardly fail to fertilize itself" ("Fl. and Ins.," p. 46). Muller, "Fert. of Fl.," p. 143.

If, however, the anthers are examined when they reach that position, it will be found that, with the exception of a very few pollen globules, the mere husks of the anthers alone are left. The self-fertilization of the stigmas must consequently, as we have found it, take place before the stigmas have reached this last position, and not as a consequence of their reaching it.

The close similarity in the construction of the two flowers, *M. sylvestris* and *rotundifolia*, is naturally a strong argument in itself, irrespective of any actual observations, in favour of the method of their fertilization being likewise similar, and that there can be no such distinction between

these kindred flowers, that "*sylvestris* cannot fertilize itself," and that *rotundifolia* "can hardly fail to do so." *M. rotundifolia* consequently gives confirmatory support to the evidence given above against the statement that in *M. sylvestris* "cross-fertilization is secured."

CHAPTER XVI

CONSPICUOUS AND HIGHLY COLOURED FLOWERS AND DINGY FLOWERS

"THAT many flowers have been rendered conspicuous," Darwin says, "for the sake of guiding insects to them"—and so affecting cross-fertilization—"is highly probable and almost certain" ("Cr. and S. F.," p. 386). "In the case of all large and highly coloured flowers," Lord Avebury tells us, "the pollen is carried from flower to flower by the agency of insects" ("Fl. and Ins.," p. 8).

These statements by no means accord with the facts connected with our English flowers. In illustration of this, we cite a dozen of our brightest and most conspicuous common flowers, which are rarely, and in some cases never, visited by bees at all, and rarely even by insects, in comparison with the number of flowers.

Daffodils (*Narcissus Pseudo-Narcissus*).
Dwarf Furze (*Ulex nanus*).
Primroses (*Primula vulgaris*).
Cowslips (*Primula veris*).
St. John's Worts (*Hypericums*).
Buttercups (*Ranunculaceæ*).
Marsh Marigolds (*Caltha palustris*).
Anemone (*Anemone nemorosa*).
Daisies (*Bellis perennis*).
Ox-eyed Daisies (*Chrysanthemum leucanthemum*).
Corn Marigolds (*Chrysanth. segetum*).
Wild Chicory (*Cichorium Intybus*).[1]

[1] This list might be much extended as the Elder (*Sambucus niger*); the greater Stitchwort (*Stellaria Holostea*); the Germander Speedwell (*Veronica Chamædrys*); the deep blue Marsh Gentian (*Gentiana Pneumonanthe*), and many others.

Every hymenopterist, we feel assured, would say that if he was to limit himself to these flowers his collection at the end of a year would be almost nil. We speak here particularly of the *Hymenoptera aculeata*, the division of the bee family.

The bright and most conspicuous yellow *Daffodils* are never visited. We have on many occasions passed through woods where there were millions of the flowers, the woods even yellow with them, and portions of some fields as well, and yet have never seen a bee of any kind upon any one of them. On one occasion we saw a brimstone butterfly visit a flower. Though living not far away from these woods of daffodils, and so visiting them when the flowers were in their fullest bloom, such was all the result. In fact, at the season when the daffodils are in bloom, few bees are upon the wing, and, when an occasional one was seen in the woods, they were always upon the early sallows.

It is impossible that the Petty Furze or Whin (*Ulex nanus*), which covers some waste fields with a mass of yellow bloom, should be generally fertilized by bees or insects. It is in flower in the last weeks of August until the end of the first or second week in November. During its last eight weeks of blooming, a bee is scarcely to be seen abroad, yet the sandy and heathery commons are often yellow with bloom, and the flowers produce an abundance of pods.[1]

The bright-yellow St. John's Worts (*Hypericums*), which are some of the brightest and most conspicuous flowers, the hymenopterist will search almost in vain to meet with bees

[1] Our Common Gorse (*Ulex Europæus*) in comparison with its vast number of flowers at the height of its season, is likewise but partially visited by bees. In the earlier months, more bees may be seen upon it on account of the scarcity of other flowers. It produces very little nectar, and consequently the bees are comparatively very few that visit it. This is still more noticeable, as it possesses a strong odour.

upon the flowers. The flowers are destitute of nectar. H. Müller says, "In all self-fertilization occurs in default of insect visits, and is without doubt the usual mode of reproduction in the most conspicuous forms." From our observation, the visits of insects are exceptionally rare. Large garden hypericums are occasionally tested by bees, but they are no true criterion of what occurs in the fields. "Fert. of Fl.," pp. 141, 142.

Every one who walks through our pasture fields, when they are bright with the golden-coloured *buttercups*, cannot but notice how rarely he sees a bee or even a fly upon the flowers in comparison with the number of flowers. Their nectar is probably distasteful to all insects, and the pollen generally unused as well "from the presence of acrid matter so common in the *Ranunculaceæ* ("Cr. and S. F.," p. 431). It is the same with the Marsh Marigold (*Caltha palustris*) [1] and the Anemone, members of the same order of *Ranunculaceæ.*

The Daisies and Chrysanthemums we shall meet with in our next chapter.

The conspicuous blue Wild Chicory—a colour which is by some considered to be peculiarly attractive to bees—is in our experience almost absolutely unvisited.

There are two other very conspicuous flowers, though we have not placed them in the list above, yet we cannot but mention them in this connection. One is the Red Poppy (*Papaver rhœas*). The flowers secrete no honey. They are, however, visited occasionally by bees either in the vain search for nectar, or for the sake of the pollen. But the flowers do not need the visits of insects for their fertilization.

[1] Müller says in reference to the Marsh Marigold (*Apis mellifica*) "in hundreds collecting pollen." We have never seen such an occurrence, though we have observed thousands of the flowers. Our attention was once called to *Ranunculus philinotis* by bees visiting it. This seemed so unusual that we examined the plants. We found the calices and some of the leaves covered with honeydew. It might have been such an exceptional attraction in Müller's marsh marigold.

The pollen of *Papaver rhœas* is shed on the stigmas before the flower opens at all, and at that stage the stigmas from the circumference to the centre are usually coated with pollen. H. Müller says of it, "The numerous anthers stand close round the stigmas, and dehisce before the opening of the flowers." It was fully productive even under Darwin's net ("Cr. and S. F.," pp. 365, 366). The other flower is the exquisitely deep-blue Marsh Gentian (*Gentiana pneumonanthe*). Blue flowers, as we have said above, are supposed by some writers, as the late Mr. Grant Allen, to have reached the acme of "progressive colouration" under the influence of insects, and to be their special favourites. We have met with this gentian in abundance growing in one of our southern counties intermixed amongst the heather, the flowers of which the bees were visiting, but we never saw a bee alight upon the gentian.

"Fert. of Fl.," p. 93.

Mr. Meehan tells us, that "the flowers of the Rocky Mountain region are beautifully coloured, and the paucity of animal life of all kinds in the Rocky Mountain region is well known, but there is no more scarcity of seed in the coloured flowering plants there than elsewhere. Nearer home we see the same thing. In many of our woods spring flowers abound, but any observer of woodland flora must have been struck, especially in spring, with the rarity of insects about them. But all these plants, without any remarkable exception, seed well."

The Garden (London), vol. x.

If it were true what Darwin tells us, that "if insects had not been developed upon earth, our plants would not have been decked with beautiful flowers;" or that which Lord Avebury states, that "to bees flowers are indebted for their colour" ("Fl. and Ins.," p. 51), it seems strange that, after they have produced these coloured flowers, they should neglect and almost cease to visit them. To dwellers in the temperate zone, if Mr. Wallace is correct in his prognostications, there is a sorry prospect, as he tells us that "there

"Origin of Species," p. 151.

is good reason to believe that, if the insect races should all become extinct, flowers (in the temperate zone at least) would soon dwindle away, and that ultimately all floral beauty would vanish from the earth" ("Darwinism," p. 332). In another passage in the same book, Mr. Wallace writes, "My whole experience in the equatorial regions of West and East has convinced me that in the most luxurious parts of the tropics flowers are less showy than in temperate climates: bright and showy flowers are, as a general rule, altogether absent. In Aru, in the Malayan Archipelago, all had blossoms of a green or greenish-white tint, not superior to our lime trees. In the regions of the equator, whether forest or savannah, a sombre green clothes universal nature. Yet insects of striking brilliancy are found everywhere there." "Darwinism," pp. 490, 491.

This latter testimony seems to us quite to refute the idea that insects are the cause of floral colouration as in equatorial regions insects most abound, and yet by the statement above the flowers remain of a "sombre" hue.[1]

Dingy Flowers.

Colour and conspicuousness evidently in the above flowers play but small part in favouring cross-fertilization. They stand also in direct contradiction to Darwin's statement, "I have found it an invariable rule that where a flower is fertilized by the wind" (as these flowers almost unexceptionally are) "it never has a gaily coloured corolla." "Origin of Species," p. 151.

Kerner tells us, that "it is by smell that humble or other

[1] The proboscis of bees (and of insects generally) is not a sharp inoculating lancet, but a most tender and delicate lapping and sucking instrument, and the laminæ of the maxillæ of bees if they even irritate or rend the floral portions of the plant, yet they would not affect in any way the essential character of the seed.

"Flowers and their Unbidden Guests," p. 195, *n*.

Wood, "Episodes of Insect Life."

bees are attracted to the nectar. The nectar of flowers, it is true, makes as a rule no impression on our olfactory nerves, but this by no means excludes the possibility of its being perceptible to insects even at some distance." "It is the odour of flowers rather than their appearance," Mr. Wood tells us, "by which both bees and butterflies would seem to be enticed."

Professor Plateau of the University of Ghent, in his book "Comment les fleures attirent les insectes," concludes that "colour plays a very subordinate part in attracting insects to flowers." After many and various experiments, he arrived at the definite conclusion that "insects seem to care little either for the presence or absence of floral parts of brilliant colours. Nectar and pollen is what they seek; they are guided but very slightly by sight, but in a sure way by some sense, which can only be called smell."

In confirmation of this view stand the dingy flowers. Many green, brown, dingy and dull-whitish flowers are the greatest favourites of bees, and perhaps no flowers of a showy aspect, not even excepting the dandelions in the early spring, are more constantly visited by them. Such dingy or dull-whitish, or greenish, flowers, as the lime, black currant, gooseberry, raspberry, ivy, Japanese ivy (*Ampelopsis*), common buckthorn (*Rhamnus. catharticus*), alder buckthorn (*R. frangula*), sycamore, holly, figwort, asparagus, hare's-foot clover (*Trifolium arvense*), bear evidence to the fact that it is scent and honey, not colour, which pre-eminently affect the visits of bees.

Our first notice of the common Buckthorn (*R. catharticus*) was caused by the humming of bees. We were passing a hedge-row composed entirely of this shrub in June, and the humming of the bees was as loud as that heard under lime trees in flower, and it so attracted our attention that we examined the cause. We found that the small inconspicuous flowers on the shrubs had attracted

them. It was the same with the Japanese ivy (*Ampelopsis*). We had never noticed its flowers until our attention was called to them by bees. We accidentally, in August, entered a small court in Merton College, Oxford. It seemed as if a swarm of bees had taken possession of the court. The sun was shining upon the wall on which the *Ampelopsis* was growing, and the abundant nectar of the flower was the great attraction to them, though the flowers themselves were so inconspicuous that they had to be sought for amongst the leaves to be seen.[1]

If bees had such power as to the colouring of flowers as that attributed to them by Darwin, all these dingy ones mentioned above, with very many others, must, through the constant visitation of them by insects, have attained through all their ages of existence to a conspicuous colouration.[2]

[1] The *Ampelopsis* in many situations and seasons does not flower at all, or rather, more correctly, does not bring its flowers to perfection. The buds show, but often drop off without opening at all.

[2] With the facts above, connected with flowers—many gaily coloured flowers neglected, many dingy flowers particularly visited, by bees—Professor Plateau consequently asks, "if insects are not attracted to flowers by their gay colours, can we believe in the insect-selection theory as to the origin of flowers?"

CHAPTER XVII

"FLAGGED" FLOWERS

Bentham's "English Flora," p. 285.

"The most extensive family among flowering plants, which is also represented in every quarter of the globe, and in every description of station, is the *Compositæ*." There are, according to Dr. Ludwig Pfeiffer, over 10,000 genera of flowering plants, and of these 1000 belong to the Compositæ, and the genera have an exceeding number of species.

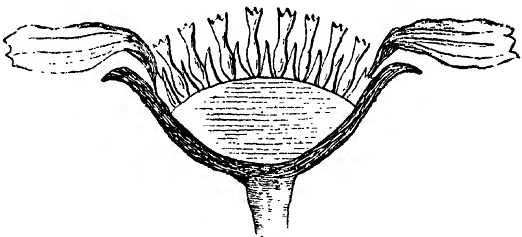

FIG. 9.—Chamomile (*Anthemis*). A capitulum or head of a flagged composite flower, with florets, and scales between the florets. The florets are not arranged so closely packed as in the naturally growing flowers.

This is an order which, by the arrangement of the stamens and pistils, is most particularly framed for the *self-fertilization* of the flowers. The flowers of the Compositæ appear in heads (Capitula). Each head is a cluster of small flowers or florets packed closely together, and not one large compound flower, as the name would seem to imply.

The name ("Compositæ") is applied because the heads in all the species, as in the Daisy, contain within an external

covering so many florets. Each floret is, with the exception of those in the ray, a perfect flower with stamens and pistils; the ray floret, when present, has pistils only, and sometimes not even pistils. The number of these separate perfect florets in a single head of the Daisy (*Bellis perennis*) averages from 50 to 80; those in the Dandelion (*Taraxicum officinale*, Linn.) from 70 to 100, or even occasionally more; in the Ox-eye Daisy (*Chrysanthemum leucanthemum*) the number averages from 400 to 500.

The Order of the Compositæ is divided into three divisions; there is a fourth division, but it does not occur in England. These three divisions are—

1. The *Corymbiferæ*. This division has all the central flowers tubular and yellow. They generally have an outside rim of flat and oblong rays, usually white, though sometimes yellow or purple. The typical form of this division is the *Daisy*.
2. The *Cynarocephalæ*. The florets in this division are all tubular and regular; there is no ray. The typical flowers of the division are the *Thistles*.
3. The *Cichoraceæ* or *Ligulates*, in which all the florets are flattish and oblong or ligulate. Of this division the *Dandelion* is a typical form. This division receives its name from the Chicory (*Cicorium Intybus*), in which all the florets are ligulate, as in the Dandelion.

Our observations will be confined to the first division, and to those flowers, consequently, which have a ray like the Daisy.

These flowers, from the conspicuousness of their rays, are said to be "flagged," and it is asserted that the "flagging" serves for the "attraction of insects" in order to secure the cross-fertilization of the florets. That this is the purpose of the "flagging" many of the flowers distinctly contradict.

It would scarcely be necessary to go beyond the Daisy to establish this. In our experience, we have never seen more than three or four bees during a whole season settled on the flowers. Flies even are, comparatively with the number of flowers, rare visitors. This has been our experience after observing year after year thousands of the flowers. This, we feel assured, would be the experience of every one who would only carefully observe them. The flowers close at night, so no night-flying insect can visit them. Moreover, the flowers bloom some time before insects appear, and continue to bloom and to produce seeds when all insects have disappeared. The propagation and extension of the Daisy is consequently quite independent of any "flagging" in order to attract insects for their cross-fertilization. Yet what flowers, save perhaps the buttercups alone, equal, much less surpass, in numbers this very common flower?

There are other members of these specially "flagged" flowers which are almost equally unvisited by the bees or their congeners: as the Great White Ox-eye (*Chrysanthemum leucanthemum*), and the still more conspicuous Yellow Corn Marigold (*C. segetum*). These flowers are generally much neglected by insects. We have found, upon the thousands and thousands of these flowers which we have passed through, occasionally a hive-bee, and several species of Prosopis, Halictus, and Sphecodes. These are very small bees, and their visits, in comparison with the vast number of the flowers, are exceedingly few. The flowers of the *Corn Marigold* continue to bloom, and to set their seeds through October and November, when all bees are gone, and when flies, even, are scarcely seen. It must also be remembered that each head contains over 400 florets, which renders visits by small bees and other small insects still less influential for any effective fertilization of the head.

Mr. T. Meehan, speaking of his experience in America, says that he had "never seen a winged insect on the Ox-eye Daisy, though on the grounds near him they were in bloom by the thousand; every little floret perfected a seed. There were millions and millions of seeds, and even admitting that there might be some winged insects that he did not see, they were certainly so scarce that it was out of the question to suppose that each of these had been fertilized by winged insects." *Proceedings of the Academy of Nat. Science of Philadelphia,* 1876.

Of the scentless Chrysanthemum (*C. inodorum*, Linn.) H. Müller says, "The only visitors of this flower that I have noticed are two: a chrysis and a fly." "Fert. of Fl.," p. 331.

The Yarrow or Milfoil (*Achillea millefolium*), a member of the same division of *Compositæ*, is cited by Lord Avebury as a flower "rich in honey, and much visited by insects" ("Fl. and Ins.," p. 119). In this we think that Lord Avebury is particularly astray. We have observed thousands of these flowers, but we have never, except on two or three occasions, seen a bee upon the flowers; yet the Milfoil is on every roadside, the commonest of flowers, and in bloom all the summer and autumn through, and so at a time when all the Hymenoptera (bees and wasps, etc.) are upon the wing, yet, day after day the summer through, such is the result of our observation. Other flowers of this division, as the Common Camomile (*Anthemis nobilis*) and the Common Matricary (*Matricaria camomilla*), are most rarely visited, yet they are conspicuously "flagged." The same may be said of the very brilliantly coloured flowers of the genus *Inula*, the Fleabane, and the Golden Samphire (*I. dysenterica* and *I. crithmoides*). Many others of this division of the Compositæ might be mentioned to the same effect. The chief exception to this non-visitation of "flagged" corymbifers by bees occurs in those members of the genus Senecio, which are "flagged," as the Common Ragwort (*Senecio Jacobæa*). This is a particular favourite

with many of the smaller wild bees, as species of Colletes, Prosopis, Halictus, and Sphecodes ; and with many of the Fossores (or Diggers) as Pompilus, Salius, Ammophila Entomognathus, Crabro, and others. The florets doubtlessly abound with honey which is agreeable to them, and which is easy of access.

Lord Avebury gives us, from H. Müller (“ Fl. and Ins.,” p. 113), a tabular list of the number of different species of bees, etc., which visit some of the Compositæ. We only take out of it a single instance, that of the Milfoil (*Achillea millifolium*). H. Müller records 30 different kinds of bees, 27 moths or flies, and 30 kinds of insects belonging neither to the bees, nor flies, nor Lepidoptera, upon the Milfoil. This does not in any way invalidate our own observations, as 30 different kinds of bees might be seen on the Milfoil in the course of 15 years, during which time H. Müller's observations were made. To judge of the influence of bees or insects on certain flowers, the flowers must be constantly observed during the height of their flowering season ; and if thousands of the flowers are passed day after day, and an insect or bee is only occasionally seen upon them in comparison with the number of flowers passed, it is a sure sign that insects or bees have very little influence in effecting the cross-fertilization of such flowers.

‘ Fert. of Fl.,” p. 336.

Moreover, it must be remembered that compound flowers (*Compositæ*) contain many florets in each head. In some flowers, as in the Daisy, as we have already mentioned, the average number of florets is 50 ; in others 400 ; and in this flower (the Milfoil) the average is from 20 to 30 florets. A single visit of an insect would contribute but very little towards the fertilization of the head.

The mere accumulation of lists of insects seen on flowers —as given by H. Müller, in his *Fertilization of Flowers*— during a considerable number of years, is apt to be very misleading as to the real amount of insect visitation in

comparison with the number of flowers. On a favourably situated pale or post in a garden in the course of a single summer, 20 to 30 or more different kinds of insects may be seen casually settling and sunning themselves. If we, in reference to the insect-visitors of the *primrose*, had made a statement of the insects which we had seen upon it similar to those made by H. Müller, it would have been—

Insect Visitors.—Apidæ, Anthophora pilipes; *Andrenidæ*, Andræna nigroænea; *Bombylidæ*, Bombylius discolor; *Thysanoptera*, Thrips; *Coleoptera*, Chrysomela (?); *Lepidoptera*, Brimstone Butterfly (Gonepteryx Rhamni); Cabbage Butterfly (Pieris brassicæ).

This enumeration would have given a very misleading indication of such visits, and might have led those who read it to suppose that such visits were constantly by those insects repeated, whereas (taking no account of Thrips which inhabit the flowers) the rest were each confined to a single visitor. It was quite an event for record to see a visitor amongst tens of thousands of the flowers.[1]

[1] Moreover, in these lists of H. Müller, we have no distinction drawn as to their possible influence between the visits of bees (*Hymenoptera aculeata*) and the visits of Flies (Diptera), and Beetles (*Coleoptera*). These insects are very sparsely provided with hairs for carrying pollen. The Beetles are almost entirely unprovided with a carrying apparatus. Yet these two orders often furnish two-thirds of the list. This may be seen, for example, in the lists attached to the Daisy (p. 321), the Ranunculus (acris, repens, and bulbosus)—our common meadow buttercups (p. 76)—the Milfoil (p. 328), and many others. Moreover, even the one-third left of those belonging to the bee tribe, more than half of the species mentioned as visiting the above flowers—the Daisy, buttercups, and Milfoil—belong to the minute genera of the Halicti, small Andrenæ, Prosopis, and Sphecodes. Many occur on the lists which in England, at least, are rare, and some exceedingly so. Such, in our experience, might be met with once a month, or once a year, or once in a lifetime. (A special instance of this last kind we had two days after the above was written. We caught *Andræna tridentata* upon *Lythrum salicaria*. This bee we had never met with previously. Mr. Saunders, in his "Hymenoptera

We have said that the anthers and pistils in the florets of the *Compositæ* are arranged particularly for their *self-fertilization*. The anthers are united together and form a circular tube (Fig. 10); they burst inwardly, and on the inside of this tube the pollen collects, and through this tube the stigmas, as the style elongates when the pollen is ripe, are, as seen in the accompanying diagram (Fig. 10), forced. This arrangement of stamens and pistils is found not only in the Flagged Division, of which we are here more immediately speaking, but in the members of the two other divisions. So what is here said of the one division, applies equally as to fertilization to all the *Compositæ*.

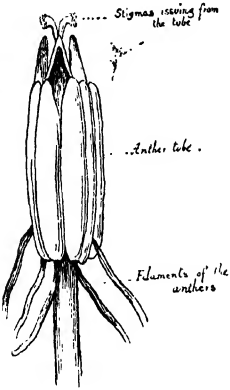

FIG. 10.—Anther tube of one of the Compositæ.

The styles terminate in two stigmas, and usually the stigmas are tipped with what has the appearance of a brush of hairs. They act like a chimney-sweeper's brush, brushing, in its upward progress, the pollen up the staminal tube. It has been affirmed by Mr. A. H. Hassell, that these hairs at the ends of the stigmas are not hairs merely, but are *essentially* concerned—"having stigmatic functions"—in the fertilization.

"Annals of Nat. Hist.," vol. viii.

aculeata," only records two instances as previously met with in England, and he describes it to us as "very rare.") Yet all similar insects are catalogued in Müller's lists. Such insects, as agents in effecting cross-fertilization, should be excluded from such lists. A much surer method for arriving at a valid conclusion is, as in the cases of the Daisy, the Buttercups, and Milfoil, to walk through the fields, and to notice, in them, or on the roadside, on propitious days, and during the morning hours, the number of such insects met with in comparison with the numbers of the flowers.

In this important paper Mr. Hassell states his conclusion, that not only the surface of the true stigma, but that portion of the style itself which is covered with hairs in the (*Campanulaceæ* and) *Compositæ*, is essentially concerned in the fertilization of the florets. Representations of these hairs can be seen in H. Müller's drawing of the stigma of the Autumnal Hawkbit (*Leontodon autumnalis*).

But the arrangements for the self-fertilization of the Compositæ are complete without them. We have said above that the stigmas are forced through the anther tube when the pollen is ripe. As the pistil rises in the anther tube, and approaches the top of it, the stigmas begin to be separated from each other by a very slight interval, which, when it is passing the top of the tube, becomes, in the majority of cases, "a cleft," and in this cleft the pollen is deposited from the mass which has been forced out of the tube as the pistil advanced (Fig. 11). "In the Dandelion division (*Cichoraceæ*), some of the grains of pollen," Professor Henslow says, "mostly fall into the cleft." But even before the anther tube has opened at the top—for the anther tube, like the floret itself, is covered over at first by its five-toothed border, the teeth of which are seen in Fig. 10—and before the stigmas can be touched by insects, pollen grains can be seen on the borders of the stigmatic junctures. "In the Groundsel (*Senecio vulgaris*), the stigmatic arms are often retained below, but separate, within the anther tube, and so self-fertilization is secured." "In this flower," H. Müller says, "self-fertilization takes place regularly. The pollen grains swept out by the hairs at the tip of the style, remain partly on the edge of the stigmas, and partly upon the

FIG. 11.—Cleft in the stigma of one of the *Compositæ* (*Corymbifer*), covered with pollen as it issues from the anther tube.

"Popul. Science Review," vol. iii. New Series.

Ib.

inner surfaces when they separate. It is certain that this self-fertilization is effectual, for the plant is fully productive even in periods of bad weather, when it is assuredly not visited by insects." "Fert. of Fl.," p. 336.

The opportunity of the stigmas being fertilized with their own pollen precedes the opportunity of fertilization by insects. In fact, if the pollen were conveyed from one floret to another, the pollen so conveyed would fall on florets which had already been fertilized either before, or as, they issued from the anther tube. Even if insects did so convey pollen to other florets on the same head (*capitulum*), this would be no more, as Professor Henslow says, "than equivalent to self-fertilization." "Popul. Science Review," vol. iii. New Series. Darwin, even with his strong advocacy of cross-fertilization as superior in effect to self-fertilization, still often expressly states that "a cross between two flowers on the same plant does no good, or very little good" ("Cr. and S. F.," p. 449).

After we had written the above, we met with Mr. Meehan's conclusions on the subject. He says, "a careful examination of the Dandelion (*Taraxicum officinale*, Linn.) and Ox-eye Daisy, showed that they were self-fertilizers. In the Dandelion, as the pistil grew, it carried the pollen with it. The apex of the pistil then forked, and a watcher could see that, as the cleft opened, the pollen on the line of the cleft fell in. It was but a little, but that was enough. In the Ox-eye Daisy the pollen fell into the stigmatic cavity more easily than in the Dandelion. Insects might visit it subsequently; it would make no difference, having already received its own pollen." *Proceedings of the Academy of Nat. Science of Philadelphia*, 1876, pp. 109, 110.

Mr. Meehan adds that the hairs of the stigma of one floret so curve over that they are almost certain to fertilize, with the pollen they carry, the adjoining florets, if unfertilized by themselves; and he speaks to the same effect as Professor G. Henslow above, that this would be "no more than self-fertilization, as they all have the same food, the

same light, and the same condition of life, in every material effect." In such flower-heads there could be no prepotency of the pollen of one floret over that of another.[1]

The three divisions of the Compositæ are thus peculiarly furnished for *the self-fertilization of their florets.*

Though the stigmas are thus fertilized at an early period in the Compositæ, yet they continue to grow (and to curve backwards over the florets), like the stigmas of the Travellers' Joy (*Clematis vitalba*), the Mallows, and other flowers.

Lord Avebury could scarcely have carefully examined the florets when he wrote the following sentence, "When the stigma has attained its full length, the two branches open and curve downwards so as to expose the stigmatic surfaces which had *previously been pressed closely to one another*, and thus protected from the action of the pollen" ("Fl. and Ins.," p. 120. The italics are ours).

Darwin experimented on one species of *Compositæ* only. This was a Lettuce (*Lactuca sativa*). "The season was unfavourable, and I did not," Darwin says, "obtain many seeds either on the covered or uncovered flowers. A nurseryman, on whom I could rely, told me that he had been in the habit of sowing several kinds of lettuce near together for the sake of the seed, and had never observed that they became crossed" ("Cr. and S. F.," p. 173, *n.*).

This experience of the nurseryman accords with the arrangement of the anthers and stigmas recorded above, which, as we have seen, almost excludes the possibility of the florets being cross-fertilized. Darwin, without any support even from his experiment, and in direct contradiction to the experience of the nurseryman, on whom he

[1] H. Müller tells us that "the Dandelion has fully retained (!) the possibility of self-fertilization, since it begins to bloom so early that, as a rule, its first flowers receive no insect visits, whilst its latest flowers are also liable to be left unvisited." "Fert. of Fl.," p. 359.

said he could rely, yet strangely says "the Compositæ are well adapted for cross-fertilization"! (Ib., p. 173, *n.*).

The Corymbifers evidently, from the above facts, do not need "flagging" in order to attract bees and insects for their fertilization, as the fertilization takes place before they could affect the florets at all.

On the other hand, the rays of the Corymbifers appear particularly designed for the protection of the florets.

At the earliest stage of all in the Corymbifers, whilst the florets are still young, tender, and immature, these rays remain folded over the disk. In some cases, after the full expansion of the flower, when the rays have done their work of protection, they remain permanently open. In other cases, such as that of the Daisy, these rays at night, and on dull and sunless days, bend over and re-enclose the florets.[1]

It is the same with members of the Compositæ, as the Dandelion and Yellow Goat's-beard (*Tragopogon pratense*), both belonging to the division of the Ligulates; the latter has among country-people the name, from its habit of closing about midday, of John-go-to-bed-at-noon. Hildebrand states that the "ray florets of the Compositæ last for a long time, until all those on the disk are fertilized" ("F. Fl.," p. 5). From these circumstances there can be but small doubt that the rays are not for flags to insects, but for the protection of the florets. Though Darwin thinks that the rays are to attract insects, yet he says that "they are, however, of service in another and very different manner, namely, by folding inwards at night and during cold rainy weather, so as to protect the florets of the disk." "Kerner," Darwin says, "clearly shows that this is the case" ("F. Fl.," p. 6, *n.*).

The ray florets have no anthers, and are fertilized from

[1] It receives its name of Day's-eye from the characteristic of being open in fair weather from sunrise to sundown, and closing at night.

the outer row of the tubular florets. The pollen of the outer row of florets and the stigmas of the ray closely adjoin; they are at maturity at the same time; the slightest breath of wind would carry the pollen. These outer florets contain no honey nor pollen, so that they have no attraction for bees or insects.

The extreme abundance of the Compositæ depends in greatest measure, in our opinion, not on the conspicuousness of the flowers for the attraction of insects, nor on the possession of a pollen mechanism "which renders cross-fertilization certain in the event of insect visits," as stated by H. Müller, and followed by Lord Avebury ("Fl. and Ins.," p. 118), but on the provision for the sure self-fertilization of the florets; by the seeds of very many of the order being provided with a feathery pappus (which is very noticeable in such flowers as the Dandelion, Groundsell, Coltsfoot, and John-go-to-bed-at-noon (*Tragopogon*) with its most exquisite parachute), so that the seeds are wafted in every direction by every breath of wind; and by the number of seeds which each capitulum in most of the flowers produces, so that if many seeds perish, some few, from their capacity for travelling, would be deposited upon soil favourably adapted for their vegetation.

CHAPTER XVIII

CONTRADICTORY RESULTS OBTAINED BY DARWIN AND OTHER EXPERIMENTERS

We here notice a few of the divergent and contradictory results arrived at by Darwin and by other experimenters with respect to the same flowers; these divergencies arising doubtlessly from the different methods adopted by different experimenters in their experiments.

The first case that we notice is the divergence in results between Hildebrand and Darwin in their experiments on *Primula sinensis*, *Pulmonaria officinalis*, and *Linum grandiflorum*.

When Darwin and Hildebrand experimented separately on *P. sinensis*, Darwin found (to quote only two cases from Tables 10 and 11, "F. Fl.," pp. 39, 41), when the long-styled form was fertilized by pollen of the short-styled, that—

The average number of seeds per capsule was . 50

But in a similar experiment by Hildebrand—

The average number per capsule was . . 41

When the short-styled form was fertilized by pollen of long-styled—

The average number of seeds per capsule was by Darwin . 64

" " " " Hildebrand . 44

Darwin says, "Hildebrand's plants were kept *in a room*, or under other unfavourable conditions, for his capsules in almost every case contained a smaller number of seeds than

mine" ("F. Fl.," p. 41). Darwin tells us that Hildebrand thought that "the difference of our results may be accounted for by his plants having been kept in a room, or never having been shaken" ("F. Fl.," p. 42).

H. Müller says that "Darwin found that in the absence of insects, the long-styled form of *P. sinensis* was 24 times as productive as the short-styled, and that Hildebrand found *both absolutely barren.*" "Fert. of Fl.," p. 383.

The same divergence in results occurs in their experiments with *Pulmonaria officinalis.* To quote Darwin, "We thus see that the English long-styled plants, when illegitimately fertilized, were *highly fertile;* whilst the German plants, similarly treated by Hildebrand, were *completely sterile.* How to account for this wide discordance in our results I know not. Hildebrand cultivated his plants in pots, and kept them for a time *in his house,* whilst mine were grown out-of-doors, and he thinks that the difference of treatment may have caused the difference in our results" ("F. Fl.," p. 103. Italics are ours).

The same results are seen in comparing Darwin's and Hildebrand's experiments on *Linum grandiflorum.* Darwin, under his net, obtained a moderate amount of seed from the flowers fertilized by their "own form" pollen; whereas those of Hildebrand, similarly fertilized, "did not produce any seed" ("F. Fl.," pp. 86, 87).

In these experiments, of the two unnatural methods adopted, that of Darwin's in the open air seems to be less unnatural than that of Hildebrand in his house; in consequence, Darwin had "a greater fertility in seeds."

Nor were such contradictory results limited to heterostyled flowers. Professor G. Henslow points out a similar contradiction between the results obtained in the experiments of Darwin and H. Müller in other orders of flowers. He says, "Whilst Mr. Darwin includes the *Foxglove* and *Yellow Toadflax* amongst the self-sterile plants, H. Müller

"Floral Structures," p. 216, *n.*

considers them both to be self-fertilizing." Darwin says, "The Foxglove is extremely sterile, only a few poor capsules being produced" ("Cr. and S. F.," p. 363). With this view Hildebrand agrees (Ib., p. 82). Müller says, "The flowers almost always bear seed, even in long-continued rainy weather, and therefore it is probable that self-fertilization is effective. Hildebrand's experiments are no evidence to the contrary."

"Fert. of Fl.," p. 438.

Darwin even makes contradictory statements about this flower. As quoted above, he says that it is "extremely sterile" when insects are excluded, yet he records an experiment of his own in which he fertilized six flowers with their own pollen under a net in his garden, and "all produced good capsules," and no difference could be seen between their seeds and those of flowers on the same plants which were cross-fertilized and also "produced good capsules" ("Cr. and S. F.," p. 85).

We cannot but feel that Müller's conclusion was the correct and natural one. There can be no possible difficulty in the self-fertilization of the Foxglove, as the stigma is surrounded by the anthers; and as it is mature whilst the anthers are mature, and the stigmas separate during the time that the pollen is being shed, Hildebrand's experiments, as Müller says, "are no evidence;" they were conducted in a closed room.

There are other instances of contradictory results in Darwin's volumes, as between himself and Gärtner and Mr. Scott of Edinburgh. We quote only one in each case. "Gärtner," Darwin says, "has shown that certain plants of *Lobelia fulgens* are quite sterile with pollen from the same plant, but none of the plants on which I experimented were in this condition" ("Cr. and S. F.," p. 179, *n.*). We have already given the contradictory results of Mr. Scott and Darwin in reference to *Primula scotica* in Chap. IV. above.

Of Köbreuter's and Gärtner's experiments Darwin says, "These two most experienced observers who have ever lived arrived at diametrically opposite conclusions in regard to some of the very same forms." "Origin of Species," pp. 221, 233, 234.

Herbert came to opposite conclusions to both Gärtner and Köbreuter. Herbert had great advantages, Darwin says, from his extensive hothouses.

We will close with the case of *Eschscholtzia Californica*, in which the results of three experimenters all differed from one another. Ib., p. 222.

The product of the flowers of this plant, protected under a net by Darwin, was, to those unprotected, as 71 to 100; with Hildebrand, as 11 to 100. H. Müller found all his plants completely self-sterile ("Cr. and S. F.," p. 332).

Various, doubtlessly, would be the causes of such contradictory results as are recorded in this chapter. They would be influenced by the atmospheric conditions of the particular seasons, weeks, days, or hours when the experiments were made. They would also have been greatly influenced by the different methods adopted by each experimenter, and especially when, as in many of Darwin's cases, only a single experiment with the flower was made. The examples given are quite sufficient to show how unreliable artificial experiments are for giving any true indication of what occurs under natural conditions.

Greenhouses, hothouses, or a closed room, or a house are generally more injurious to natural fertility even than Darwin's net.

CHAPTER XIX

WANT OF PARALLELISM IN THE RESULTS OF DARWIN'S OWN EXPERIMENTS—LEGUMINOSÆ

Conflicting results were met with, not only by different experimenters on the same flowers, but contradictions and want of parallelism, in esults, occurred with Darwin himself in his own experiments. "Even with individuals of the same species," Darwin says, "some were utterly sterile; others moderately so; and some perfectly self-fertile" ("Cr. and S. F.," p. 312).

This want of parallelism is singularly exhibited in his experiments with member of Pea-flower family—the Order of the *Leguminosæ*. To this Order of the *Leguminosæ* we shall, with one exception, exclusively confine our remarks on this subject, though there are many other genera and species of the orders experimented upon by Darwin, in which the results were almost equally conflicting and equally divergent.

The corolla, in all the *Leguminosæ* of our native species, consists of 5 petals (Fig. 12): an upper one, which is called the "vexillum," or "standard," and which usually sooner or later turns backwards, or is reflected; two lateral petals or "wings;" and two lowest ones, united at their interior or lower edges into a boat-shaped form, and called in consequence the "carina" or "keel." This latter lies between the two wings. In this keel the stamens and pistil are enclosed.

In all the flowers of this order the pollen is ripe, and

shed at a very early stage, even when the flowers are but half-grown. When shed, the pollen falls into the keel, and is there stored. This ripening of the pollen takes place in all the flowers before the vexillum is reflected (Fig. 15), and so the stamens and stigmas are at this stage protected against all contact with insects. The stamens usually consist of 2 sets of 5 each—a longer and a shorter set.

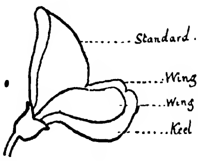

FIG. 12.—A flower of the Leguminosæ in its advanced stage with standard reflexed.

In the fertilization of these flowers the wind is a most important agent, by shaking the flowers and thus bringing the loose pollen on the stamens, or that which is lying in the keel, in contact with the stigma. The importance of this agency in the economy of these flowers is, as we have previously noticed, indicated by the slender pedicles, either principal or secondary, on which they grow. Without such shaking, in many of the species the pollen would remain partly on the stamens or at the bottom of the keel, and not come in contact with the stigma at all.

Out of 23 species of this order, which Darwin experimented upon, he classed 11 species under his division of "Plants sterile without insect-aid," and 12 species he classed under his division of "Plants fertile without insect-aid" ("Cr. and S. F.," pp. 357, 369).

Bird's-foot Trefoil (*Lotus corniculatus*). Darwin says generally that "papilionaceous flowers are specially adapted for cross-fertilization" ("Cr. and S. F.," p. 153), and he classes *Lotus corniculatus* particularly amongst "flowers sterile without insect-aid." He does not give any special description of the method of fertilization of this flower, as he does of some other members of this order, as of the Broom, which we shall meet with below. He classes it as above, and merely says, "Several covered-up plants produced

only two empty pods, and not a single good seed" (Ib., p. 361).

But those who followed Darwin's opinions in extremely pressing cross-fertilization in the floral world, as H. Müller and Lord Avebury, have elaborated a "piston-mechanism," working under the agency of bees, for effecting the cross-fertilization of this flower, whilst Nature has most simply provided for its self-fertilization, anterior to, and quite irrespective of, any gratuitous assistance by insects.

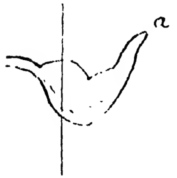

Fig. 13.—The keel of *Lotus corniculatus*. All to the right of the line is a closed cone, excepting a small outlet at *a*.

Of this plant H. Müller says, "The anthers dehisce in the bud, whilst both the keel and wings

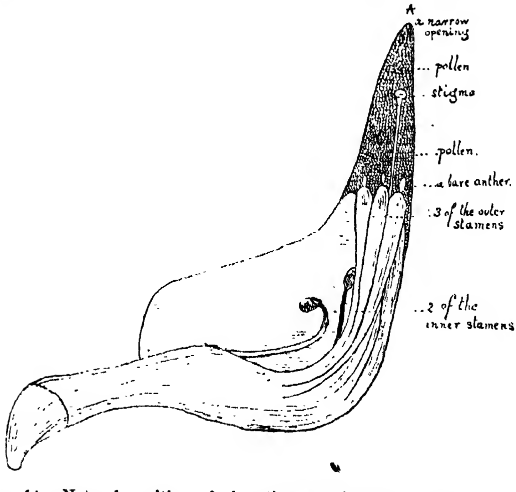

Fig. 14.—Natural position of the stigma amidst the pollen when the *Lotus corniculatus* is in the bud. The right half of the keel removed, and the stigma shown closely invested by the compressed pollen much magnified.

are still covered by the standard, and before any of the

petals have nearly attained their full size." That this is the case the slightest examination of a half-grown flower will show. The keel is remarkably narrow for some little distance towards its top, its upper portion forming a cone (Fig. 13). The stigma lies at about one millimetre from the end of the tip (Fig. 14). "Fert. of Fl.," p. 168.

The stamens consist of two sets of 5 each—an inner and an outer set. Some time before the flower is fully grown, and whilst the standard is still unreflected (Fig. 15), the pollen is ripe. At this time, all the stamens are of the same length, and whilst they are in that position the inner set shed their pollen. When the pollen of the inner set is thus being shed, the filaments of the outer set become dilated (Fig. 14). They still continue to grow, until their pollen is shed, so that they thrust the pollen of both sets of anthers forward towards the stigma, and retain it in that position, "their thickened ends," Müller says, "tightly closing in the base of the hollow cone (Fig. 14). The entire space between the thickened filaments and the top of the keel is filled with compressed pollen." The stigma is thus surrounded by, and brought in contact with, the pollen, and is necessarily subjected to fertilization. During this time the keel, from the end of the thickened stamens to the tip, remains tightly closed, with the exception that a small opening exists at the very tip (A in Fig. 14), where the sides of the petals forming the keel lie in contact with each other, but are not united. Ib., p. 169

FIG. 15.—Flower of *Lotus corniculatus* before the vexillum is reflected,' in which the anthers are already burst within.

Notwithstanding this natural arrangement for the self-fertilization of the stigma, by its lying in the midst of, and so being covered with, pollen, cross-fertilization is assumed to take place through bees alighting on the wings of the Ib.

"Fert. of Fl.," p. 169. flower, and so depressing the keel that a kind of "piston-mechanism" is set in action, through which a portion of the pollen, and in some cases the top of the pistil, is forced out at the tip of the keel and against the breast of a visiting bee, which comes to it laden with pollen from other flowers.

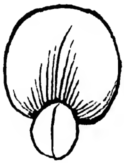

FIG. 16.—Front view of *Lotus corniculatus*, showing keel completely covered over by the wings: the keel itself invisible from above.

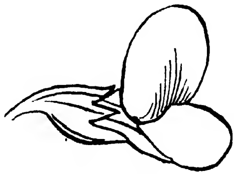

FIG. 17.—Side view of the same showing the keel entirely covered by wings.

In the ordinary action of a bee, Müller says that only the pollen is forced out, "but if the bee forces its way further into the flower, the stigma protrudes from the apex of the carina and rubs against the ventral surface of the insect." This may be true, but still there is the difficulty as to how this protrusion of the stigma could be seen, as the bee's body, when it visits the flower, entirely covers the keel. No ocular proof of such protrusion of the stigma on such visits could be obtained. It must consequently be a mere supposition of its possibility. Nor can trial be made exactly resembling the action of a bee.

Ib., p. 70.

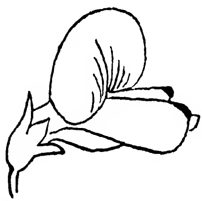

FIG. 18—Showing the position of wings and keel of *Lotus corniculatus* after fertilization.

Sowerby, in his great illustrated work of English flowers, says of the *L. corniculatus*, "the wings are nearly straight on the upper margin, they are *connivent and contiguous* at the upper edges." The wings also extend slightly beyond and overlap the tip of the keel, as seen in Figs.

Sowerby's "Eng. Botany," vol. iii., pp. 64, 65.

16, 17. Consequently, when the bee alights upon the wings, they are pressed together by the legs of the bee, and they thus cover over the keel, and usually would necessarily, by their intervention, prevent all contact of the stigma, even if it were pressed out of the keel, with the under surface of the body of the bee.

There is also a still further impediment, from the structure of the flower, to this contact with the bee taking place.

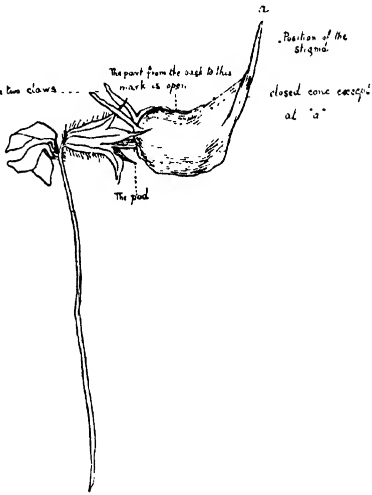

FIG. 19.—Keel of the Lotus still covering the pod with the stigma after the pod is half-grown.

a.—At "*a*" is a narrow opening.

There is in the Lotus, at the base of the wings, a firm ball-and-socket joint; a projection from the inner surface of each of the wings fits into a deep, corresponding depression on the outer sides of the keel. This ball-and-socket joint is in Fig. 17 concealed by the standard. This holds the wings and the keel strongly together. Any depression of the keel by an alighting bee would be accompanied by a

corresponding depression of the covering wings. It is this ball-and-socket mechanism, together with the "connivent and contiguous" upper edges of the wings, which prevents the bees from depressing the keel separately from the wings, which is mentioned by Darwin as occurring in the Sicilian Sweet Pea (*Lathyrus odoratus*). Of this latter flower, Darwin says, "that insects should sometimes fail to cross-fertilize these flowers is intelligible, for I have thrice seen humble-bees sucking the nectar, and they did not depress the keel petals so as to expose the anthers and stigma; they were quite insufficient for fertilizing the flowers" ("Cr. and S. F.," p. 155). This impediment to the exposure of the stigma applies with greater force to the *Lotus* than to *Lathyrus odoratus*, as in the latter flower the keel is open on its upper surface along its whole length, whereas in Lotus it is closed completely except at its extreme tip (Fig. 13). This overlapping of the keel by the wings continues until the flower gives signs that the period of its maturity is past, and that its fertilization has taken place. The whole flower then becomes relaxed. The wings begin to separate at their upper surface, to loosen their grasp on the keel, to wrinkle and to shrink, so that the tip of the keel becomes visible and projects beyond them, as in Fig. 18. All visits of bees after the tip of the keel thus becomes exposed could have no influence on the fertilization of the flower; that has already taken place. If the pod is opened just before this final stage of the relaxation of the wings, the ovules will be found well developed within.[1] The keel,

[1] Delphino advances, for the fertilization of this flower, a more extravagant supposition. He considers that the stigma does not become capable of fertilization until its papillæ have been slightly abraded. The pollen with which it had been covered in the keel must be rubbed off, and at the same time itself abraded by its passing through the opening at the apex of the keel, and foreign pollen at the same time deposited upon it by the visiting bee. This, without any proof, seems to be a far-fetched idea indeed, especially as

as seen in Fig. 19, very often remains until the pod is more than half-grown.

We think that the advocates of the "piston-mechanism" theory are driven to seize upon the small outlet at the tip of the keel—which seems to us as Nature's own provision for the ventilation of the cone in order to preserve the pollen in a healthy condition—as a *dernier ressort* for their theory of the cross-fertilization of a flower, which Nature has most completely furnished, and at an early stage, with every possible contrivance for its self-fertilization. Such a supposed method seems a positive displacement of the natural arrangements of the flowers, and makes the flowers dependent upon the mere accident of the stigma being extruded and coming in contact with the under surface of the body of a possible pollen-laden bee. Plain, obvious natural facts in such a supposition are, in our opinion, ruthlessly set aside merely to satisfy a theory.

Moreover, for any validity in such a theory, even if the flowers' own pollen were displaced by foreign pollen, it has still to be proved that such foreign pollen is prepotent over the pollen of its own flower which has been long in contact with the stigma. Müller allows that "this is hard to prove by direct observation." [1] "Fert. of Fl.," p. 170.

the edges of the opening in the keel through which the stigma would pass are very smooth and very tender, and could not possibly cause any abrasion of the stigma even if it did pass through. Moreover, we do not see, in the aspect of the stigma of *L. corniculatus*, why it should be differentiated from other stigmas of the order in "not being capable of fertilization until its papillæ have been slightly abraded."

[1] We have already noticed in Chap. XVII. the misleading effect of Müller's mere accumulated lists—accumulated during a series of years—of insect visitors to flowers. This is very noticeable in his list of insect visitors to the *L. corniculatus*. He tells us that bees, and especially those with abdominal collecting brushes, are the chief fertilizers of this plant (p. 171). In his list, 10 bees, with abdominal collecting brushes, *i.e.* bees belonging to the division of *Dasygastræ*, are

Darwin] experimented upon this flower. The result recorded is as given above. "Several covered-up plants produced only two empty pods, and not a single good seed" ("Cr. and S. F.," p. 361). This was a very natural result under his net. It is a low-growing and partially decumbent flower, usually averaging from 4 to 8 inches in height. It would be quite unshaken, and probably the pollen would not arrive at perfect maturity, under the net. Yet from this experiment the *L. corniculatus* is placed in the division "Flowers sterile without insect aid." "Often," Meehan tells us, "on a single experiment, Darwin's theory was founded."

"Nature," vol. xv. p. 138.

We consider this a curious instance (among many) in which a secondary agency is made to displace a primary one, in order to advance a mere theory, where Nature has so obviously provided for the self-fertilization of the flowers.

The Common Broom (*Sarothamnus scoparius*). We have already seen in Chap. IV. how the Common Broom, a member of this order, was under Darwin's net perfectly sterile in all its flowers, excepting those "which were dis-

catalogued as visitors. Only 5 of those mentioned occur in England. With us there are 18 species of such bees belonging to the two chief genera of this division (Dasygastræ), Osmia and Megachile, and 12 species of these are rare or local (Saunders, *Hymenoptera aculeata*). In our experience during the last year we have not met with a single instance of such bees upon the Lotus. You may pass through pasture fields where the flowers are innumerable and not see one such bee upon the flowers. Others may meet with them upon the flowers, but we feel that their experience would coincide with our own that to meet with such bees upon the Lotus in comparison with the number of the flowers is quite exceptional. The hive-bee is the chief visitor amongst bees, and it has no abdominal brush. Even Nomada and Cœlioxys are catalogued—rare parasitic bees—and they have no long hairs at all upon their abdomen, which is as smooth and polished as that of wasps. Even Diptera (Flies) are mentioned in the catalogue, and Müller includes one that he says he "only observed once." We mention these facts that no undue weight in the matter of insect fertilization may be given to such accumulated lists.

turbed by being beaten by the wind against the surrounding net" ("Cr. and S. F." p. 360). Yet this plant, though fertile in the flowers which were thus beaten, and protected from insects, is placed—in spite of this protection and fertility—amongst the 11 species which were "sterile without insect aid."

We should not have thought it necessary to notice this flower again, after this clear evidence to its self-fertilization, had not Darwin thus classed it as "sterile without insect aid," and said that "the flowers are adapted by a curious mechanism for cross-fertilization so that cross-fertilization is almost rendered inevitable" (pp. 163, 164).

The stamens in this flower, as in *L. corniculatus*, consists of two sets of 5 each, a shorter and a longer set. In the unopened flowers the anthers of the stamens lie in closest contact with the pistil and in close contiguity with the stigma at its extremity. The pistil has "a long flattened spoon-like extremity" which curves round and comes in contact with the anthers as they lie in the keel. This spoon-like extremity of the pistil, whilst it is still in the keel and the flower unopened (with the vexillum unreflected), becomes actually on its inner surface in many cases positively plastered with ripe and loosened pollen. Darwin notices the fact of the spoon-like extremity of the pistil being thus covered with the shed pollen, for he says, that when the pistil comes out of the keel by the alighting of the bee upon the flower "the pistil rests for a time on the back of the bee, and leaves on it the load of pollen with which it is charged" (p. 164), and that the stigma is at the same time "rubbed against the

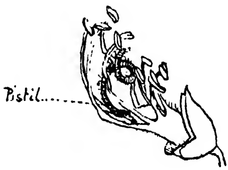

FIG. 20.—The position of stamens and curled pistil of the Broom, whilst the flower is still in the bud and the standard unreflexed; pollen is seen deposited upon the pistil; the keel is removed. (After Sowerby.)

back of the bee, dusted with pollen from the long stamens, either of the same or another flower." He also tells us that when the bee alights "the short stamens spring out which rub their pollen against the abdomen of the bee" (p. 163). "By this mechanism," Darwin continues, "cross-fertilization is rendered almost inevitable, and we shall immediately see that the pollen from a distinct plant is more effective than that from the same flower" (p. 164).[1]

Now there are several objections to the validity of this conclusion.

The first, and chiefest, is that the ripened and shed pollen lies in extraordinary quantity in the keel and on the "flattened, spoon-like pistil," and surrounds the stigma in the keel. The buffeting of the wind alone is needed to bring the pollen in contact with the stigma. In the wild

[1] We quote in full in this note the passage in which the method of the cross-fertilization of the Broom is described by Darwin.

"The flowers of the Common Broom," Darwin says, "are adapted by a curious mechanism for cross-fertilization. When a bee alights on the wing-petals of a young flower, the keel is slightly opened and the short stamens spring out, which rub their pollen against the abdomen of the bee. If a rather older flower is visited for the first time (or, if a bee exerts great force on a younger flower) the keel opens along its whole length, and the longer as well as the shorter stamens, together with the much elongated curved pistil, spring forth with violence. The flattened, spoon-like extremity of the pistil rests for a time on the back of the bee, and leaves on it the load of pollen with which it was charged. As soon as the bee flies away, the pistil instantly curves round, so that the stigmatic surface is now upturned and occupies a position, in which it would be rubbed against the abdomen of another bee visiting the same flower. Thus, when the pistil first escapes from the keel, the stigma is rubbed against the back of the bee, dusted with pollen from the long stamens, either of the same or another flower; and afterwards against the lower surface of the bee dusted with pollen from the shorter stamens, which is often shed a day or two before that from the longer stamens. By this mechanism cross-fertilization is rendered almost inevitable, and we shall immediately see that pollen from a distinct plant is more effective than that from the same flower" (pp. 163, 164).

flowers, consequently, grains of pollen are almost invariably found upon the stigma some time before the flower has opened. At the stage at which it is seen in Fig. 20, it is curled upon itself, and is unelastic. When the fertilization of the flower has taken place, the pistil begins to enlarge and lengthen out, and as the stigma portion uncurves, it presses against the end of the keel. The flower then sooner or later explodes; which it does either automatically, or from a bee alighting on it at the explosive stage. Its explosion is a sign that the flower is fertilized. After the pistil springs forth, the keel, as Professor Balfour says, "finally falls down."[1] If the rudimentary pod is examined at that time, the ovules within will be found well developed. All this takes place before insects could usually touch the stigmas at all. It would be quite exceptional for the stigma to come in contact with foreign pollen before its own self-fertilization in the keel.

"Systematic Botany" (*Sarothamnus scoparius*)

Another, but minor objection to Darwin's interpretation, is that the shorter stamens, which Darwin tells us "rub their pollen on the abdomen of the bee," have parted almost entirely with their pollen before they can escape from the keel on the advent of a bee. These shorter stamens do, as Darwin tells us, "shed their pollen a day or two before the longer stamens." When the shorter stamens issue from the keel, the husks of the anthers, with possibly some few pollen grains attached, alone remain upon the filaments. They could therefore have but small influence, if any, in supplying the abdomen

[1] Darwin says, "If the visits of bees are prevented, and if the flowers are not dashed by the wind against any object, the keel never opens, so that the stamens and pistil remain enclosed" (p. 164). Such a result as the keel not opening was due to Darwin's net. The flower remained unfertilized, and the pistil ceased to grow, and so the keel remained unforced. On large Broom bushes, in favourable seasons, and on hot days, the automatic opening of the keel may not unfrequently be seen.

of the bee with pollen in sufficient quantity for effecting efficiently in any supposed case cross-fertilization in other flowers.

Darwin tells us that the Broom is "incessantly visited by bees." This is very different from our own observation of the flowers. It is visited by them (and more particularly when it first appears in bloom, from the scarcity, at that season, of other flowers), but only very partially, in comparison with the vast number of flowers which each plant produces, and which at the height of the season are in bloom together. We have constantly observed this on the solitary bushes growing by the roadside or in the fields. We have also on repeated occasions gone through a very large clump of Broom bushes, covering a thousand square yards, when in full bloom, at the end of May or the beginning of June, and when there were tens of thousands of flowers out upon them, and yet it was only an occasional bee, one here and there, which could be seen amongst them. The cause of this partial neglect by the bees in comparison with the number of flowers, is accounted for by H. Müller's observation that "the flowers do not secrete nectar" ("Cr. and S. F.," p. 164).[1]

In watching the bees on the Broom bushes, we have noticed that frequently, where they force their way into a flower on which the standard is only partially reflexed, they do not cause the keel to open, so that the bees leave the keel, as in *Lathyrus odoratus*, mentioned just above, in the same state as it was before their visit. The bees, we have also noticed, will frequently visit five, six, or even a dozen

[1] Though H. Müller says that "the flowers do not secrete nectar," yet there must be some minute substance (as Darwin observes) acceptable to the bees at the root of the staminal tube, though outside of it (since the tube is monadelphous), which induces the bees in their visits to probe the bottom of the open flowers. The smallness of the amount is the probable cause of their partial neglect of the flowers.

exploded flowers, when the season is fully on, to one into which they have to force their way. On these exploded older flowers there is no pollen left, but the mere husk of the anthers alone remains at the top of the filament.

Even if the complicated method propounded by Darwin for the fertilization of these flowers were valid, still the fertilization for effective results would be dependent on many accidental circumstances: viz. that the flower should be visited by a bee; that it should be visited neither at too early, nor too late, a stage, as in the first case neither stamens nor pistil would leave the keel, and, in the latter case, one or both sets of anthers would be almost destitute of pollen; and that the longer stamens should regularly strike with their anthers the back of the bee, which though it might occasionally occur, is, as far as our observation goes, by no means a regular occurrence. We cannot recall an instance of having seen it ourselves.

Nor does the experiment to which we are referred—"we shall immediately see that the pollen from a distinct plant is more effective than that from the same flower"—give any valid support to such an opinion. The experiment is the following.

Darwin compared the produce of the flowers of the Broom grown in the open air with the produce of those grown protected from bees under a net. The average produce of the pods from flowers grown in the open air, and which he tells us "had been fertilized by bees," was 7·14 seeds per pod. The average from flowers spontaneously fertilized on a large bush, which had been covered up, but which had been much agitated by the wind, was 2·93 seeds per pod" ("Cr. and S. F.," p. 164).

The results from such an experiment are very inadequate to establish the conclusion that "pollen from a distinct plant is more effective than that from the same flower." The close-meshed net over the bush would in a very great

measure annul the influence of the wind; the minimizing of the solar rays would measurably deteriorate the pollen, and the stimulus of the rays being in a great measure withdrawn, would necessarily affect the growth of the pollen tubes for the fertilization of the ovules. Darwin's own statement in reference to such an experiment, entirely dissipates the validity of such a comparison. "Plants thus protected," Darwin says, "yield very few pods in comparison with those produced by neighbouring uncovered bushes, and sometimes none at all" ("Cr. and S. F.," p. 164).

In spite of the facts given above in favour of the self-fertilization of the flowers; in spite of the facts which render any amount of cross-fertilization very improbable; and in spite of the flowers, when favourably situated under the net, being perfectly fertile, Darwin placed the flowers of the Common Broom (*S. scoparius*) as "flowers sterile without insect aid."

This flower, again, is, in our opinion, a curious instance in which a secondary agency is made to displace a primary one—in order to advance a mere theory—when Nature has so obviously provided for the self-fertilization of the flowers, and where *proof* of that self-fertilization was obviously given to Darwin in his own experiment.

We now come to plants, not only of the same order whose *genera* are divided off from one another, but to plants of the same *genus* whose species are divided off from one another, into fertile, and sterile, without insect aid.

The Common Vetch (*Vicia sativa*) is fertile without insect aid (p. 367).

The Bean (*Vicia Faba*) is sterile without insect aid (p. 360).

"The unprotected plants," Darwin says, "of *Vicia Faba* were three or four times more fertile than the protected ones" (p. 360). But Müller tells us that "Darwin found the fertility of the Bean (*Vicia Faba*) reduced to a third

when insects were excluded by a net; but if the flowers were shaken, they produced good and well-filled pods, though still protected from insects." "Fert. of Fl.," p. 207.

Yet notwithstanding this, the Bean is placed by Darwin in the sterile division.

The separation of the species is even more marked in the Trefoils. Of the four absolutely indigenous species classed, two are placed in the self-fertile division, and two in the self-sterile. We will take one of each.

The Hop Clover (*Trifolium procumbens*) is "fertile without insect aid."

The Red or Purple Clover (*Trifolium pratense*) is "sterile without insect aid" (p. 361).

We have already fully treated the Red or Purple in Chap. IV. We here merely repeat the result of Darwin's experiment upon the flowers. "One hundred flower-heads of the Red Clover," Darwin says, "on plants protected by a net did not produce a single seed, whilst 100 heads on plants growing outside the net yielded 2720 seeds."

Irrespective of other considerations given in Chap. IV., which show the invalidity of such a result, we have instanced the perfect self-fertility of the flowers in New Zealand and Australia, where there were no humble-bees to cross-fertilize them at all.

The French Bean (*Phaseolus vulgaris*) is "fertile without insect aid" ("Cr. and S. F.," p. 367).

The Scarlet Runner (*Phaseolus multiflorus*) is "sterile without insect aid" ("Cr. and S. F.," p. 360).

A still greater abnormal want of parallelism is catalogued by Darwin as the result of his experiments with the Scarlet Runner of our English gardeners (*Phaseolus multiflorus*) and the French Bean (*Phaseolus vulgaris*), when he experimented with them under the net. The former (*P. multiflorus*) "was very partially fertile" ("Cr. and S. F.," pp. 168, 360), and *P. vulgaris* "highly fertile, when

insects were excluded" ("Cr. and S. F.," p. 153). This divergence even Darwin considered remarkable. "This difference in self-fertility," Darwin says, "between *P. multiflorus* and *P. vulgaris* is remarkable, as these two species are so closely related that Linnæus thought that they formed but one" (Ib., pp. 150, 153).

Now, it is perfectly evident, even from Darwin's own experiment, which we give, that bees are not necessary for the full fertility of *P. multiflorus*.

"Several years ago," Darwin says, "I covered some plants under a large net, and these produced on one occasion about one-third, and on another occasion about one-eighth, of the number of pods which the same number of uncovered plants growing close alongside produced. This lessened fertility was not caused by any injury from the net, as I moved the wing-petals of several protected flowers in the same manner as bees do, and these produced remarkably fine pods" (Ib., pp. 150, 151).

Now, it is noticeable, in this description of the experiment, that no pollen from another flower is introduced; the fertilization takes place under protection by Darwin moving the wing-petals—almost exactly supplying in this case the action of the wind—and so shaking the pollen on to the stigma. The flowers when thus shaken were self-fertilized, and produced "remarkably fine pods."[1]

[1] "Professor Hoffman," Darwin tells, under *P. multiflorus*, "maintains that the flowers are specially adapted for self-fertilization. He enclosed several flowers in bags; and as the buds often dropped off, he attributed the partial sterility of these flowers to the injurious effects of the bags, and not to the exclusion of insects." Then Darwin adds, "But the only safe method of experimenting is to cover up a whole plant, which then never suffers"!!

Darwin also says that "Mr. Belt gives a more curious case; the plant grows well and flowers in Nicaragua; but as none of the native bees visit the flowers, not a single pod is ever produced" (p. 151). The *P. multiflorus* is a Mexican plant, and it is not at all extraordinary that it should be sterile in Nicaragua, not from the lack of the visits

The true cause of the unnatural contrast between two members of the same genus as that which Darwin would establish in each genus of Vicia, Trifolium, and Phaseolus, by his experiments, is most probably to be attributed to the partial or almost complete absence of the wind, or sun, or both, in the one case—the case of sterility—when the flowers were maturing or mature, and the presence of the wind, or sun, or both, in sufficient power to counteract the covering of the net, at the time of the maturing or the maturity of the flowers in the other. Nature is not so contrarious in her operations as to frame two flowers almost exactly similar in their conformation for reproduction, so that one should require, and the other should be perfectly independent of, insect aid.[1]

of bees, but from being transplanted into a far hotter climate than its native soil. Such results are of very ordinary occurrence. Even of *Linum flavum*, which is only "a South European perennial" (Bentham), Darwin says, "I have inquired, but have never heard of its seeding in this country" ("F. Fl.," p. 99).

[1] There is in the species of the *Trifolium pratense* and *T. procumbens* a difference in the outward conformation of their flowers; which conformation, however, is in each an equal hindrance to insect visitors. The length of the corolla tube being, as we have already seen, the hindrance in the Red Clover (*pratense*); the standard in the Hop Clover (*procumbens*), instead of becoming reflected, as the flower grows to maturity, and as is the ordinary case in the Leguminosæ, turns in the opposite direction over the end of the keel, and so bars access generally to the flower by insects. This is the explanation of what Darwin notices. He says, "I have often watched this plant, and have never seen the flowers visited by insects" ("Cr. and S. F.," p. 368). If Darwin had noticed the cause, he would never have continued, "I suspect that the flowers of this species are frequented by small nocturnal moths," as the same cause which kept away insects by day would keep away also their congeners by night.

The Black Medic (*Medicago lupulina*) of another genus of the Leguminosæ presents a contrast to the Hop Trefoil, though the two flowers are almost exactly similar in colour, size, and number of florets in the head—from which circumstance the two flowers are often confounded until the coiled pods of the Medic appear—in

Moreover, the *Order of the Leguminosæ* is, of all natural orders, the richest in cleistogamic flowers. "They are more common in this family than in any other" ("F. Fl.," p. 314). All cleistogamic flowers are abundantly fertile, and are, in our opinion—they will be mentioned more particularly below in Chap. XXIII.—an evidence of the natural self-fertility of the open flowers of the plant on which they are found. Thus the genus *Vicia* and *Trifolium* both produce these perfectly self-fertile cleistogamic flowers ("F. Fl.," p. 313; "Fl. and Ins.," p. 91), whereas Darwin, as instanced above, separates species belonging to each of these genera from each other into fertile, and sterile, without insect aid. The want of parallelism in these flowers of each genus did not exist in Nature, but arose from Darwin's method of experimenting.

Darwin's idea that irregular flowers are "specially adapted for cross-fertilization" ("Cr. and S. F.," 153) is contradicted by this large order of irregular flowers, "the most extensive order after the composites of all the natural orders of flowering plants." "When a flower is irregular," Darwin says, "this implies that they have been specially adapted for fertilization by insects" ("F. Fl.," p. 339). This idea has been repeated, and in some cases extravagantly pressed by those who accepted it after him. Lord Avebury says, "It is probable that all flowers which have an irregular corolla are fertilized by insects" ("Fl. and Ins.," p. 86). To carry out this idea Lord Avebury even forces this cross-fertilization upon *Ononis* (the Restharrow), a member of the Leguminosæ, and says, "Ononis is exclusively fertilized by bees" (Ib., p. 92). Yet Lord Avebury also tells us that "Ononis does not secrete honey" (Ib., p. 91). It has consequently nothing to attract bees to visit it. "The conspicuousness of the corolla," as Darwin

Bentham, "English Flora," p. 155.

having its standard reflected, and so being constantly visited by hive-bees.

observes, "does not suffice to induce repeated visits from insects unless nectar is at the same time secreted" ("Cr. and S. F.," p. 425). This, too, Lord Avebury allows, "Bees rarely visit flowers unless for some real advantage" ("Fl. and Ins.," p. 14). It has, moreover, all its stamens bound into a single bundle (Monadelphous), so that bees could not introduce their proboscis into the tube to extract the nectar even if it produced any. It is also with this genus, as with the other members of the Leguminosæ which we have mentioned, that the pollen and stigma are mature, and the former shed whilst the flower is still unopened. We have only once seen a bee (*Bombus lapidarius*) visiting Ononis. It settled on two flowers, made a short examination, and almost immediately, though there were very many flowers, flew away.[1] Ononis is also one of the genera given in Darwin's list as bearing the fully productive cleistogamic flowers. We cannot conceive how it could be said of such a flower that "it is exclusively fertilized by bees."

Of all flowers, the Leguminosæ might be said to have the least need of insects to assist in their fertilization. The pollen is ripe, and shed at a very early stage, some time before the standard is reflexed, and until it is reflexed no insect can gain entrance to the flower. The keel also acts as a natural reservoir for the pollen; into it the pollen falls, and in it, in many of the flowers, accumulates. The least play of the wind on the plant or on their slender pedicels would at once land it upon the stigmas, and this long before it could be touched by insects. It is exceedingly difficult to obtain absolute evidence for the invariable self-fertilization of flowers. But in this Order of Leguminosæ the Sweet Pea (*Lathyrus odoratus*), Darwin tells us, "seems invariably to fertilize itself. I conclude that

[1] *Onomnis minutissima* is given by Darwin as "fertile without insect aid" ("Cr. and S. F.," p. 367).

this is so, as five varieties, differing greatly in the colour of their flowers, but in no other respect, are commonly sold, and come true; yet on inquiry from two great raisers of seed for sale, I find that they take no precautions to insure purity—the five varieties being habitually grown close together. As no variability can be detected in plants raised from seeds, the parents of which have grown during many successive generations in close proximity, we may infer that they cannot have intercrossed" ("Cr. and S. F.," pp. 153, 151). It is the same with the Common Pea (*Pisum sativum*). "I have observed the flowers," Darwin says, "for thirty years, and in all this time I have only thrice seen bees of the proper kind at work, such as were sufficiently powerful to depress the keel" (Ib., p. 161), yet, as all know, it is abundantly productive.

Treviranus's opinion was that "self-fertilization was the general rule in the Leguminosæ." He declined to accept the results of Darwin's experiments "because the nets sheltered the plants from the movement of the air." [1]

Müller, "Fert. of Fl.," p. 217.

It is most probable, though the Leguminosæ are so especially framed and provided for self-fertilization, that some of the flowers are more or less, to a limited degree, affected by insects; it is also certain that some, as the Sweet Pea (*Lathyrus odoratus*), are, generation after generation, absolutely unaffected by them; it is very improbable indeed that any of the Leguminosæ can be classed, as Darwin has classed them, as "sterile without insect aid."

We have hitherto limited ourselves in illustration of the subject of this chapter to the *Leguminosæ*. We shall, in further illustration of the subject, refer to one example in another order, that of the *Resedaceæ*, and to this example for reasons which we shall see below. The plant (*Reseda*

[1] On the ground of this objection, the validity of which we have already seen in these pages, H. Müller "thought it needless to discuss" the arguments of Treviranus!

odorata) is adduced by Darwin, from the result of his net experiments, as a proof that "with plants of the same species and parentage, some individuals are self-sterile, and others self-fertile."

Darwin covered, during the summer of 1868, seven plants of the foreign—"native Egyptian" (Bentham)—sweet-scented Mignonette (*Reseda odorata*) under separate nets, and called the plants A, B, C, D, E, F, G. Some flowers on each plant were fertilized with pollen from flowers of their own plant; other flowers on each plant were crossed with pollen from a different plant. "They all appeared," Darwin says, "quite sterile with their own pollen, but fertile with that of any other plant" ("Cr. and S. F.," p. 336). "The flowers," he says, "were reciprocally crossed in various ways, several flowers on each of these plants being fertilized with pollen from several of the other plants" (p. 337). It is not quite clear to us from this whether more than one pollen was used with some of the flowers, or only one in each case.[1] The result, however, was that the flowers

[1] We have said that it is not quite clear to ourselves whether Darwin used more than one pollen to some of the crossed flowers, or only one in each case. We are strongly inclined by the above description to think that he applied several pollens to some of the flowers.

Darwin named, as we have said, the plants A, B, C, etc. He says, on p. 336, "Fourteen flowers on A were crossed with pollen from B or C. Ten flowers on C were crossed with pollen from A, B, D, or E." The other three cases are phrased similarly to the last. From this it would naturally seem that only one pollen was applied to each flower. But if so, the sentence which we have quoted above, which occurs on the next page (p. 337), is very perplexingly expressed. "Several flowers on each of these plants," are Darwin's words, "being fertilized with pollen from *several* of the other plants" (the italics are ours). If the pollen of one flower only was applied to each crossed flower, we should have expected the sentence to run "several flowers on each of the plants being fertilized with pollen from *one* of the other plants." But it is not so expressed. The subject is not without its importance, as if several pollens from different plants were used

were sterile when fertilized with their own pollen, and the crossed ones were fertile. However extraordinary such a result must be considered in face of the facts which we shall meet with below, yet even in this experiment there were exceptions. Three out of the above 7 protected plants produced capsules without any artificial fertilization whatever. There were altogether 7 such capsules on flowers which had not been in any way crossed. In these cases Darwin "suspects," as the flowers were near artificially cross-fertilized ones, that "a few grains of foreign pollen had accidentally fallen upon their stigmas." It seems strange that it should accidentally occur on 3 different plants, and with 7 different flowers. The result consequently fails, from these 7 self-fertilized capsules, to give any absolute support to Darwin's theory.

Under another net, at the same time, "four other plants, under the *same* large net, produced," Darwin says, "in a most capricious way, little groups of capsules." In these, Darwin "suspects" that a bee "had, on some one occasion, found an entrance, and had intercrossed a few of the flowers" (p. 337). But as the net, as Darwin frequently tells us, only admitted the tiny Thrips, a bee going through it would somewhat resemble that of a camel

to some or many of the flowers, such flowers would have a very much greater chance of meeting with a pollen sufficiently mature (under the net) than the flowers which were only once fertilized with pollen of their own plant. This repetition in the fertilization was actually practised by Darwin in his seedling experiments of this very flower, *Reseda odorata* ("Cr. and S. F.," p. 120). "It must not be supposed," Darwin there says, "that these plants produced no seed because their stigmas did not receive any pollen, for they were repeatedly fertilized with pollen." That was a case of repeatedly fertilizing with own pollen. The very same occurs again in his seedling experiments with *Reseda lutea* (p. 117). From these practices, and the above "several," we have good reason for supposing that this was the case in this experiment. If our "suspicion" is correct, then this experiment is at once null and void.

through the needle's eye. On the other hand, we are of opinion, as no bee was discovered, that these little *groups* of capsules on the four plants were more favourably situated in the net, than the other plants, in the former case, for atmospheric influences. Exactly the same occurred with exactly similar results in its kindred flower *Reseda lutea*, which we have already noticed in Chapter IV.

The next year, 1869, "four plants, raised from fresh seeds, were carefully protected," Darwin says, "under separate nets, and now the result was widely different to what it was before. Three of these protected plants became actually loaded with capsules" (p. 238). The fourth was "more self-fertile than any of the seven plants in the previous year."

In the year 1870, out of six fresh plants, self-fertilized under the net, "four became actually covered with spontaneously self-fertilized capsules, as numerous as, or very nearly so, and as fine as those on the unprotected plants growing near." Two proved almost completely self-sterile, and produced only "5 seeds of small size." Such a result might easily again have occurred from the position of the plants under the net, or from the accidental defective development of the plants.

In the year 1871, these "5 small seeds" just mentioned were placed under the net, and produced only small capsules, "some being empty, and very rarely any contained more than a single seed." What other result, we ask, could be expected from such seeds under a net? When Darwin removed the net, "the bees immediately carried pollen from one of these almost self-sterile plants to the other, for no other plants grew near. After a few weeks, the ends of the branches became covered with capsules." This result, as we see, Darwin attributed to the bees, and this notwithstanding that self-fertilized plants of *Reseda* under the net produced capsules "as fine as those on the unpro-

tected plants growing near," and notwithstanding one of his theories (mentioned in Chap. XI.) that, for cross-fertilization to supplant self-fertilization, the plants must have been grown under different conditions, for unless so grown it does "no good" ("Cr. and S. F.," p. 449). He concludes this account with a theory. "These five plants therefore inherited almost exactly the same reproductive constitution as their parents. Without doubt a self-sterile race of mignonette could have been easily established"![1]

Under the continued use of the net, Darwin could probably have continued a *race* of *R. odorata* of considerable sterility, but not, as the examples of the years 1869 and 1870 show, under natural conditions. It is not at all an uncommon occurrence to meet with occasional plants much less productive than others, especially in unfavourable years, or in unfavourable situations, or under unfavourable conditions. Every one interested in gardening is well aware of such occasional contrasts. But a self-sterile *race* would, by Darwin's own theory of the "survival of the fittest," be subject to speedy elimination. Such a dictum as that above, on such premises, "without doubt" seems pressing theories to absurdity.

The seasons doubtlessly were different, either as to the sun's power or as to the wind, in the different years when the flowers were in bloom. This is seen by Darwin's observation on the fertility of the plants in 1869; he says, "this fact"—the fertility of that year—"indicates that temperature produces some effect."

We have given this case of *Reseda odorata* in particular,

[1] It is curious that these 5 children had improved upon their parents. The 2 parents produced 3 capsules between them; here the 5 children produced 32 capsules, and 1 of these produced 18. No doubt the failure in seeds arose from the pollen tubes failing to reach the ovules, the necessary stimulus of the sun's rays were intercepted by the net.

as Darwin adduces it as "the most striking (!) instance with plants of the same species and parentage in which some individuals are self-sterile and others self-fertile" (p. 341), and then bases on that supposed divergence his theory of similar divergences in *species* of the same *genus*, saying, "it is not at all surprising that species of the same genus differ in this same manner."

We have seen in the three genera above—*Vicia*, *Trifolium*, and *Phaseolus*—which he claimed as examples of it—classing the different species of the same genus as sterile, or fertile, without insect aid—that such divergence was unsubstantiated and unreal.

CHAPTER XX

TRIMORPHIC FLOWERS

DARWIN'S theory—of a special relation between the stamens and pistils of the same length in trimorphic plants—untenable.

A. Insects not reliable agents in effecting such special fertilization.

B. Darwin's net experiments being both contradictory and unreliable, afford no adequate support to such a theory.

C. Neither a plant of one form (long-styled "F. Fl.," p. 153) grown separately; nor the barrenness of flowers fertilized under the net (Table 23, Sects. v. and vi., p. 153) with "own form" pollen, gives it any support.

D. The cleistogamic flowers directly disprove the theory.

A. INSECTS NOT RELIABLE AGENTS IN EFFECTING SUCH SPECIAL FERTILIZATION

Without entering very minutely into the case of the trimorphic forms, we shall mention some especial points in reference to them, which seem not only to invalidate Darwin's conclusions, but which show also the unreliable and uncertain basis on which his conclusions were built. We shall confine ourselves to the trimorphic flowers of the purple Loosestrife (*Lythrum salicaria*) and *Oxalis sensitiva*.

In these trimorphic plants there are three different lengths of stamens, and three different lengths of pistils in different plants. We here give a diagram of the three

different positions of the stigmas and anthers in the three different forms. The flowers are called long-styled, mid-styled, and short-styled, according to the respective position of the styles relatively to the anthers in the individual flowers. We see in Fig. 21 specimens of the three forms of the flowers.

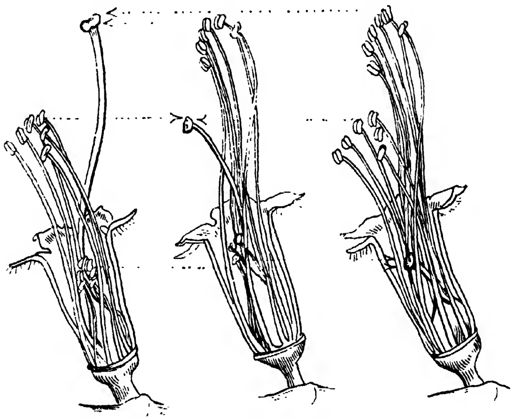

Fig. 21.—The three long-styled, mid-styled, and short-styled forms of *Lythrum salicaria*. The six methods, which Darwin called "legitimate" crossings, are represented by the arrows; for full fertility by Darwin's theory, the stigmas must be fertilized by the pollen of anthers in same horizontal line as shown by the arrows.

1. A long style with six middle and six short stamens.
2. A middle style with six long and six short stamens.
3. A short style with six long and six middle stamens.

Darwin's theory was that each stigma of the three different lengths must for full fertility be fertilized by the pollen of the stamens of the other two forms which were of corresponding length with itself. To make Darwin's theory clear, we give in the above diagram an illustration by the arrows of the cross-fertilization which Darwin considered necessary for the flowers to be fully fertile.

The purple Loosestrife (*Lythrum salicaria*) is a very common English plant. It is found on the banks of almost all our rivers, and in wet ditches, and in marshy places. It is, therefore, very accessible to all. It is in full flower in the latter half of July and in August, and continues in blossom until nearly the middle of September. The pollen of all the anthers is yellow, except in the case of the two longest sets of stamens of the mid-style and short-style forms, in which it is green.

	Flowers with long-style.	Flowers with mid-style.	Flowers with short-style.
Colour of pollen in longest stamens	...	green	green
" " mid stamens .	yellow	...	yellow
" " shortest stamens	yellow	yellow	...

The dotted vacancies which are left are occupied by the stigmas of the three forms, and indicate by their position their relative lengths and the relative position in which they stand in each flower to their anthers. The filaments of all the stamens are white before the flowers open, except in the case of the two sets of the longest stamens, which have green pollen; in these, the upper half of the filaments, whilst the flower is still unfolded, is red. The remaining portion of these filaments, and all the other filaments, gradually become red or pink, usually from above downwards, as the flower ages, until the whole of the filaments are red or pink. This is the ordinary rule with all the stamens; the long-styled, the mid-styled, and the short-styled. It is also the ordinary rule with all the pistils, as they age they become red or pink. The flowers, however, are occasionally variable in these respects.[1]

[1] Darwin states that "the stamens can be divided into three sets of a dozen each, differing from one another in the colour of their filaments" ("F. Fl.," p. 142). He also states that the filaments of the mid-length stamens of the short-styled form are "uncoloured" (p. 142). This is the case, however, only when the flowers are young. All the filaments, as we have said, become as a rule red or pink as the flower ages.

In these trimorphic flowers, the usual rule with the pollen grains is, according to Darwin, that the largest grains are found on the longest stamens; the next largest on the mid-length stamens; and the least on the shortest stamens (Ib., p. 143). They thus vary in size according to their position or exposure, similarly to the dimorphic forms in the *Primulaceæ*.

The size, however, of the pollen grains in each set is variable. Darwin tells us that "he has seen a *long-styled* plant with the grains from the mid-length and shortest anthers of the same size" ("F. Fl.," p. 149). Of the *mid-styled form*, Darwin says, "the pollen grains of different plants appeared to me in this case and in others, to be in some degree variable in size" (Ib., p. 141). Of the *short-styled grains*, Darwin says, "I examined a short-styled plant which had its grains above the average size" (p. 149).

Even the colour of the green pollen grains of the sets of longest stamens is also variable, being, as Darwin says, "sometimes pale greenish-yellow, and sometimes almost white" (p. 149). We met with a case ourselves in which the longest stamens in a short-styled plant had all the pollen grains of its anthers undistinguishable in colour from those of the set below, a whitish-yellow. What is still more singular, we met with several flowers on one plant—a short-styled one—in which three of the long stamens in one flower had green pollen, and three yellow pollen; in another, two of the anthers had yellow pollen, and in another, one had yellow. In all these the filaments were equally red in their upper half. On one short-styled plant the mid stamens had pollen of a lightest green scarcely distinguishable in colour from the longest set, the only difference being the depth of the green. In two mid-style plants, all the pollen of all the longest stamens was yellow, quite undistinguishable in colour from the shortest stamens in the same flowers.

These were met with in the middle of September. There were about six flowers on each plant open.

Thus, there is in these flowers, as Darwin says, "great variability in many important characters" ("F. Fl.," p. 149). Other points of variability we shall meet with as we proceed.

Darwin endeavours to show that by the way in which the bees alight upon the flowers, the pollen of particular anthers—as that of the longest, for instance—is deposited on a particular part of the body of each bee, and that the same particular part of the bee's body is brought into immediate contact with the long-styled stigma of another plant; that another special part of the bee is brought into special contact with the mid-length anthers, and that this same special part of the bee is brought particularly into contact with the mid-styled stigma of another plant; and, lastly, that the proboscis and fore part of the head of the bee is brought into special contact with the shortest anthers, and that this same part of the bee again particularly comes in contact with the short-styled stigmas.

In Darwin's exposition, the hind part of the abdomen of a bee, and the inside of the hinder legs carry off pollen from the longest stamens, and deposit this on the longest stigmas. The under part of the thorax of the bee, and the front pair of legs do this from the mid-length stamens, and apply it to the mid-length stigma; and the proboscis and front part of their heads carry the pollen of the shortest stamens to the shortest stigmas" ("F. and Fl.," p. 147). This arises in Darwin's opinion because "the insects which visit the flowers invariably alight upon the projecting stamens and pistils" (p. 145).[1]

Unfortunately for this idea of Darwin's—that the bees

[1] This is a point which it is difficult to determine; to ourselves they seemed to make the lower side of the calyx, as often as the stamens and pistils, their support, in sucking the flowers.

are special agents by the way in which they visit the flowers in conveying pollen, *specially from each stamen of a particular length to each stigma of a corresponding length*, and by that means effect his theory of a special cross-fertilization—there are several considerations, which, in our opinion, completely invalidate it.

The bees which visit the flowers—hive-bees, humble-bees, and other wild bees—are of very different lengths and dimensions, and have very different lengths of proboscis. Even with these conditions there might have been a certain measure of validity in Darwin's supposition, if the stamens and stigmas of the different flowers had been correspondent in each set in their length, and if the bees had visited very carefully and exactly in the same way the flowers on which they alighted, and if also the flowers had grown singly. But the stamens and pistils of the same set on different, and sometimes on the same plant, are found not infrequently to vary in length; and when in full bloom the flowers grow in dense whorls round the stem, numbering in most cases when fully developed from 6 to 20 flowers on a close-packed whorl, and with 50 to 100 flowers or more on the same spike.[1]

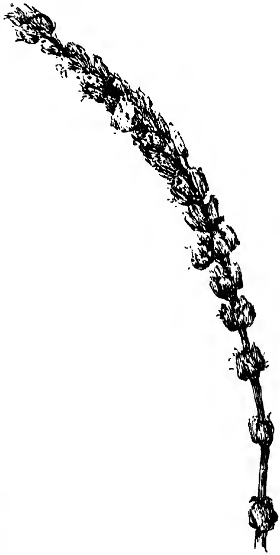

Fig. 22.—Spike of *Lythrum Salicaria* in fruit.

[1] In the accompanying diagram of a spike in fruit (Fig. 22), which is a copy of a photograph of a short-styled plant, the spike, as far as

Sometimes the greater portion of the flowers on a spike are out together, sometimes a much smaller number. Sometimes the spike from the bottom to the top is an unbroken mass of bloom; the flowers on the whorls being continuous round the spike, and the blooms on the adjoining whorls overlapping each other. The bees on their visits to the flowers vary their method accordingly. When the flowers are fully out upon the spike, both the hive-bees and the humble-bees will not infrequently crawl amongst the flowers and scramble from one to another in reckless haste—frequently crawling from the bottom to the top of a spike—so that the pollen of the various flowers over which they crawl must become attached to various parts of their bodies; and they must at the same time deposit the pollen on the stigmas of the same flowers.

Moreover, in such cases Darwin's own warning is especially applicable to the branching stems of the *Lythrum*, when the flowers are fully out upon the spike. "We should bear in mind," Darwin says of such plants, "that pollen must be carried by the bees from flower to flower on the same large branching stem much more abundantly than from plant to plant" ("Cr. and S. F.," p. 395).

The flowers have other visitors besides bees—"Various *Diptera* and *Lepidoptera*,"—with various-sized bodies and various lengths of proboscis. Their mode of movement amongst the flowers also differs. *Volucella Bonbylans*, which seems partial to the flowers, visits them in every variety of manner. Sometimes it visits from below; sometimes at the side; sometimes from above, sucking the flowers with its head downwards. But besides these, we have the *Thrips* and *Aphides*, which reside sometimes in

shown, was naturally 6 inches long. It is reduced in the diagram to 5 inches. This shows how closely the flowers are compacted together. On this spike there were 127 capsules. When spikes so packed are in full flower the spikes are almost one continuous mass of bloom.

considerable numbers inside the flowers. Whatever influence these latter insects might have, that influence would all tend to the fertilization of the stigmas by the pollen of the same flower or flowers on the same plant.

This confusion in the application of the pollen by insects becomes still further confounded, because the various stamens and pistils are very variable, not only as to their length, but as to their upturning, so that in one flower one part of a bee would be touched by them, and in another flower a different part of the bee. "The degree to which the longest and mid-length stamens," Darwin says, "are graduated in length, and have their ends upturned is variable; sometimes all are equally long. The upward bending of the pistil is variable, and especially in the short-styled form, in which it is sometimes straight, sometimes slightly curved, but generally bent at right angles" ("F. Fl.," pp. 148, 149). A great intermixture and jumble of grains must also necessarily arise from the various methods in which the bees would visit from 50 to 500 flowers of the three different forms in a single flight. Darwin says himself, "It must not be supposed that the bees do not get more or less dusted all over with the several kinds of pollen, for this could be seen to occur with the green pollen from the longest stamens" ("F. Fl.," p. 148). "From the dusted condition of the bodies of the bees which I caught on the flowers, it is probable," Darwin says, "that pollen of various kinds is often deposited on all three stigmas" (p. 164).

In consequence of this great liability of the stigmas to receive pollen of all kinds from the various insect visitors, there can be no real validity whatever in Darwin's idea, "that from these facts" (to wit, the method in which the various stamens and pistils are arranged, and in which they are inclined, and the way in which the bees visit the flowers) "it follows that insects will generally carry the

pollen of each form from the stamens to the pistils of corresponding length" ("F. Fl.," p. 148).

Darwin considered that the inclination and bending of the stamens and pistils in these flowers was brought about in order to bring them in the pathway leading to the nectary, and that this was effected through "the supreme dominating power of insects on the structure of flowers" ("F. Fl.," p. 117).

If bees had this "supreme dominating power on the structure of flowers," we should assuredly have no long monopetalous corollas bearing nectar at their base like the Red Clover (*Trifolium pratense*), which even the long-tongued humble-bees have to bore in order to acquire the nectar; no still longer corolla tubes as those of the *Primrose* and *Cowslip* excluding their visits almost absolutely; no extremely long nectar-containing spurs attached to the corollas as in the Yellow Toadflax (*Linaria vulgaris*); no troublesome arrangement of stamens as in *Erica tetralix*; no standards as in the Hop Trefoil (*Trifolium procumbens*) overreaching and overlapping the passage to the nectar-bearing part. The bees with their "supreme dominating power" would long since have remedied all such and similar impediments to their work. If they have failed to remedy these impediments, and to make them conform to their own purposes in honey-bearing flowers, what substantial reason can there be for supposing that their power has been so supreme as to place "the anthers and stigmas in their pathway" when searching for honey in the *Lythrum*?[1]

A very crucial objection to bees having more than a

[1] We are told that "humble-bees have caused long nectaries to grow, and the lips of the snap-dragon to shut; while moths have caused some flowers to keep shut all day, and so reserve their honey" (Hutton, "Darwinism and Lamarkism," p. 102). The matter in these cases seems to have been overdone by the bees. But where are the *facts* supporting such supposition?

very limited influence indeed in any fertilization of the flowers of *Lythrum salicaria*, lies in the time at which the flowers usually open and the anthers burst, and the ripe pollen becomes exposed.

In order to ascertain at what hours the flowers of the *Lythrum salicaria* chiefly opened, whether by day or by night, we gathered several branches from the *Lythrum* and put the branches in a glass with two or three inches of water at the bottom, and the results were the following as to the number of flowers which fully expanded during the night time and day time. The branches had all their open flowers snipped off at first, and on each occasion after examination. These branches were kept outside, and they had the sun upon them from 10 a.m. to 8 p.m.

		From p.m. a.m.	Flowers opened.		From a.m. p.m.	Op'd.
Branches gathered, July	26	8 to 8	68	next day, 27	8 to 8	10
The same branches	,, 27	,,	8	,, ,, 28	,,	4
Branches gathered	,, 27	,,	58	,, ,, 28	,,	8
The same branches	,, 28	,,	42	,, ,, 29	,,	11
Branches gathered, Aug.	1	,,	51	,, ,, 2	,,	0
The same branches	,, 2	,,	31	,, ,, 3	,,	0
			258			33

From this table it is evident that the flowering parts of this plant are in their most active state during the night, the numbers of flowers expanding perfectly being 258 from 8 p.m. to 8 a.m., and only 33 during the day. It was also particularly noticeable, that the anthers of the flowers which opened on each first night from 8 p.m. to 8 a.m. were almost without exception burst. It is, consequently, most probable that during the moisture of the evening, night, and morning hours, the stigmas are in their most receptive condition and that, as a general rule, the opening of the flower and its fertilization are synchronous. During these hours scarcely a bee would be found upon the wing. It is

scarcely probable that bees have much part in any fertilization of the flowers.[1]

There is one remarkable omission connected with Darwin's observations on the fertilization of these flowers. The influence of the wind, after the solar influence the most potent influence, for the fertilization of flowers, in nature, is never, in respect to the fertilization of these flowers, mentioned or even alluded to. The wind would pay no regard to any theories of Darwin. In one minute a single blast would disperse the pollen of the flowers quite irrespective of any of his theories.[2]

It is quite impossible, from the considerations given above in this chapter, to accept the opinion of Darwin that bees and other insects fulfil a *special* agency in the conveyance of what Darwin calls "the right kind of pollen" for the full fertility of these trimorphic flowers."

[1] We found in some flowers on the spikes in the fields the anthers burst before the flower itself had burst. Meehan records, "The anthers of *Lythrum salicaria* ripen usually about the same time as, sometimes before, the flower opens" ("American Naturalist," vol. xiv., p. 201).

[2] This, perhaps, is the cause of Darwin's disparagement of the influence of the wind. He most unduly depreciates its influence.

"The most important of all means," Darwin says, "by which pollen is carried from the anthers to the stigma of the same flower, and from flower to flower, are insects belonging to the Orders of Hymenoptera, Lepidoptera, and Diptera. Next in importance, but quite in a subordinate degree, is the wind" ("Cr. and S. F.," pp. 371, 372). "When insects are the agents in fertilization, and this is comparatively the more frequent case when the stamens and pistils are in the same flower, the wind plays no part" ("F. Fl.," p. 94). This supposition of Darwin's we believe to be bordering on the ridiculous. Every blast or movement in the atmosphere shakes or buffets a whole plant and all the flowers upon it at once, and that perhaps a thousand or ten thousand times a day. The bee merely visits from flower to flower. As the wind could not be made an agency subordinating its action to his theory, Darwin attempts authoritatively to ignore it.

The same omission of the influence of the wind is also very noticeable in H. Müller's "Fertilization of Flowers."

The question of such fertility is quite irrespective of the way in which bees visit the flowers, or the way in which the stamens and pistils are upturned and inclined. Such very uncertain, variable, and unreliable factors must necessarily stand aside in the inquiry—if such inquiry is to be one of any scientific value—as to whether for the full maturity of the flowers, the stigmas, as Darwin assures us, of the long-styled must be fertilized by the longest anthers, the mid-styled stigmas by the mid-anthers, and the shortest stigmas by the shortest anthers respectively.

CHAPTER XXI

TRIMORPHIC FLOWERS

B. Darwin's net experiments, being both contradictory and unreliable, afford no adequate support to such a theory.

When we examine Darwin's experiments as given in his Tables 23, 24, 25 ("F. Fl.," pp. 152–157), it is quite impossible to say that the results afford adequate support for the verification and establishment of his theory.

In the first tabulated experiment recorded there is a striking divergence in result when the long-styled flowers are fertilized by pollen from the longest stamens of the two other forms (Table 23). By Darwin's theory the two results ought to agree, as both of the two longest sets of stamens in the other two forms—the mid-styled and short-styled—are of corresponding length with the longest style, and with each of these sets of stamens he considered the union with the longest style "legitimate." But 13 flowers of the long-styled form, fertilized from the longest stamens of the *mid-style form*, produced altogether 256 good seeds:

36, 81, 0, 0, 0, 45, 41, 53, 0, 0, 0, 0, 0 = 256 good seeds.

This is an average of 19 good seeds per flower fertilized. On the other hand, 13 long-styled flowers, fertilized from the longest stamens of the *short-style form*, which is also, in Darwin's view, a "legitimate" fertilization, produced altogether 1180 good seeds:

159, 43, 96, 103, 0, 0, 114, 104, 119, 96, 99, 131, 116 = 1180.

This is an average of 90 good seeds per flower fertilized. Thus the *two legitimate crossings* (in Darwin's nomenclature) of the long-styled form differed from each other in their average produce of good seeds as 19 to 90, or as 1 to 4½.

Darwin, in his table (p. 152), when he strikes the average of the produce of each capsule in each set, does not reckon in his calculation the capsules which were barren, or produced no good seeds. Thus, in the first set, he divides the 256 seeds by the 5 capsules only which produced good seeds, so making the average per capsule of the flowers under the experiment as 51 seeds. This, however, is only the average of the produce of 5, not of the 13 flowers under the experiment. This is done irrespective of his own statement elsewhere that the efficiency of the pollen "is judged by the proportion of flowers which set capsules, or by the average number of seeds per capsule" ("F. Fl.," p. 179). Or, again, "There remains, as the best standard of comparison, the proportional number of fertilized flowers which produce capsules containing seed" ("F. Fl.," p. 229).

In the same way with the other set which produced 1180 seeds, as 11 flowers only produced good seed, Darwin divides the total by 11, so giving an average for this set of 107 seeds per capsule. These numbers, 51 and 107, Darwin adopts as his average for the two sets, instead of 19 and 90.[1]

[1] This method of calculation, as adopted by Darwin in estimating the fertilizing power of pollens, cannot be accepted as a scientific measure of the effective power of the pollen on the respective stigmas to which it is applied. Nor would it ever be accepted as a sound one for practical purposes. The amount of good seed produced by all the flowers taken together under the experiment is the only scientific measure of the effective power of the pollen on the stigmas. To take the produce of 5 flowers only, as in the first set, and to omit all the rest that produced only bad seed, cannot be a measure of the effective power of the pollen. The practical gardener would consider that the pollen which fertilized all the flowers but two, and produced 1180 good seeds, was 4½ times of more value to him than that pollen which produced, out of the same number of flowers, only 256 good seeds. He

Whichever method of calculation we adopt as to the average produce of the two sets—whether 4½ to 1, or 2 to 1 —the vast difference in the fertility given is not adequately or satisfactorily met by Darwin's statement that, "in most cases, the six stamens of each set *differ somewhat*" (!) "in their fertilizing power from the six corresponding ones in one of the other forms" ("F. Fl.," p. 160. The italics are ours). Nor is it adequately accounted for by what Darwin judged (even if correctly so, which we shall discuss below) to be the inferior potency of the mid-styled pollen in comparison with that of the other two forms.

This mid-styled pollen could scarcely have been naturally so inferior that 8 out of 13 flowers, as shown in the table above, should have produced no seed at all. To us it rather appears that Darwin's method of experimenting was the cause.

In experiments with the *mid-styled form* (Table 24, pp. 154, 155), with the pollen of stamens of equivalent length from the other two forms, which were, therefore, in Darwin's language, "legitimate unions," the results are only slightly divergent, not more so than might be expected if the experiments were made under slightly different atmospheric conditions.

In the experiments with the *short-styled forms*, when "legitimately" crossed with pollen from stamens of similar length from the other two forms, the divergence in results is again remarkable. Twelve flowers of the short-styled form, legitimately fertilized with the pollen of the shortest stamens of the *long-styled* form produced 813 good seeds :

69, 61, 88, 66, 0, 0, 56, 88, 112, 111, 62, 100 = 813,

or an average of 67 good seeds per each flower fertilized.

When the short-styled stigma was legitimately fertilized

would never, with his market valuation, be satisfied with Darwin's estimate that the effect of the 2 pollens on his pocket was only as 2 to 1.

by the shortest stamens of the *mid-styled* form, 13 flowers produced 461 good seeds:

93, 77, 48, 43, 0, 0, 69, 53, 9, 0, 0, 0 = 461,

or an average of 35 per each flower fertilized. Thus these two "legitimate" crossings of the short-styled stigma differed from each other as 67 to 35, or in the ratio of almost 2 to 1. Darwin also attempts to account for this divergence in results by supposing, as in the former case of the long-styled flowers—as mid-styled pollen was used in both—that pollen from the mid-styled form is less potent than that of the other forms. This explanation, as we shall see below, is as inadequate in this case as in the former one.

We now pass to Darwin's "illegitimate" crossings with own-form pollen.

The six experiments with own-form pollen (the two sets of pollen in each flower on their own stigmas) are all, with one exception, described "as too sterile for any average," the produce being nil or almost nil. These experiments cannot be accepted as in any way giving a fair indication of the *natural* fertility of such unions. "The term 'own-form' pollen," Darwin tells us, "here used does not mean pollen from the flower to be fertilized—for this was never used—but from another flower on the same plant, or more commonly, from a distinct plant of the same form" (p. 151). Pollen from the same plant would be grown under the net, and so would probably be immature. But it is also most probable that the "own-form" pollen from another plant of the same form was also *grown under the net.* Darwin grew two plants of each kind of Lythrum under the net (pp. 145, 150), and so from this second plant may have come the pollen which was used "from a distinct plant of the same form." If this were so, and the results, as we shall see, certainly point that way, then in all these instances the pollen would have been grown under the net, and thus the sterility met

with can be at once accounted for. However, there is, unfortunately, no distinct information given us by Darwin on this point. These sterile cases cannot, in consequence of the partial or complete use of pollen so grown, be accepted as naturally valid, and therefore need not be here further discussed, especially as we shall see below, in an experiment of Darwin's on one of the forms of this plant—the long-styled form—in the open air, which was removed from all possibility of being crossed by the other two forms, that the flowers, so far from their being sterile with their own pollen, produced, under the circumstances, a very fair average of seeds. The self-fertility of the flowers is also strongly corroborated by the cleistogamic flowers in which, as we shall see in a subsequent chapter, the anthers of each flower are the natural fertilizers of the stigma of that flower, and all the forms, so fertilized, equally produce "an abundance of seeds" ("F. Fl.," p. 329).

It is necessary that we should here give in detail the results as to the average produce of seeds of the three forms, which we found upon plants growing in the wild state, as Darwin draws several conclusions from a very limited examination of the wild flowers, which a more extended examination does not support.

"The average number of seeds," Darwin tells us, "in the three forms was ascertained by counting them in 8 *fine selected* capsules, taken from plants growing wild" ("F. Fl.," p. 143. The italics are ours). The result was that the

Long-styled capsules	gave	an	average of	93	seeds
Mid-styled	"	"	"	130	"
Short-styled	"	"	"	83	"

He says that this average, as the normal standard, was confirmed by the produce of the flowers growing in his garden, which was long-styled 80, mid-styled 97, short-styled 61 ("F. Fl.," p. 143).

The so-called "legitimate" results of Darwin's experiments *under the net* gave "for the long-styled an average of 90 seeds, for the mid-styled 117, for the short-styled 71" (p. 143).[1]

From the above results, Darwin drew the conclusion that "the mid-styled form differs from both the others in its much higher capacity for fertilization" (p. 162), and that "the mid-styled form was highly feminine in nature" (p. 163).

In our own examination we gathered several of the finest spikes of each form, and from each of the three forms selected eight of the finest capsules and counted the seeds.

The result in three different examinations was the following:—

August 17.

Long-style form: 79, 69, 90, 88, 83, 97, 79, 94 = 679: aver. 85
Mid-style form: 90, 88, 78, 90, 88, 101, 120, 109 = 764: aver. 95
Short-style form: 84, 96, 85, 89, 74, 93, 91, 88 = 699: aver. 87

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October 3.

Long-style form: 98, 88, 104, 114, 106, 103, 118, 54 = 785: aver. 98
Mid-style form: 95, 86, 77, 92, 86, 104, 58, 90 = 688: aver. 86
Short-style form: 78, 66, 100, 94, 99, 96, 77, 72 = 678: aver. 85

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[1] Darwin found, in subsequent experiments with short-styled and long-styled flowers, that they produced a much larger number of seeds than he here attributes to them. From the results of these experiments he concludes that "the normal standard of fertility for the long- and short-styled forms may have been fixed too low" ("F. Fl.," p. 209). He also says, in reference to the wild long- and short-styled forms, "I did not examine many of them" (p. 144). We must note also that Darwin's *garden* was a most unsuitable place for a test, whether the flowers were covered or uncovered, for a *strictly waterside* plant.

October 6.

Long-style form:	138, 144, 135, 127, 121, 128, 135, 145 =	1073:	aver. 134
Mid-style form:	118, 129, 124, 124, 118, 118, 136, 129 =	996:	aver. 124
Short-style form:	120, 128, 137, 117, 124, 116, 128, 130 =	1000:	aver. 125
		3069	

Our first two sets were taken from meadows in which the plants were exceedingly numerous. They grew by the side of ditches, or "lakes" as they are locally called, about five to six feet wide, the water of which was supplied from a closely adjoining river. In its lower reach the river was tidal, which caused the fresh water in this part of the river to "back up," and the height of the water in the ditches consequently varied continually during the month, though they were seldom less than two-thirds full. The third set was taken from the banks of another river some twelve miles away from the former one, where the height of the river remained almost constant: a long reach backed by a mill-dam. The produce in the last set was, as the tables show, much larger than in the first two sets, showing the great influence which position exercises on the fertility of the plants.

The results shown above diverge very considerably from Darwin's examination, particularly as to the produce of the mid-style form.

The long-style stands considerably ahead in two of the sets. The mid-style stands at the head in one set, and is on an equality only with the short-style in the other two sets. These sets certainly give no indication that the mid-style form has "a much higher capacity for fertilization than the other two forms" ("F. Fl.," p. 162); or that it is "highly feminine in its nature" in comparison with the other two forms ("F. Fl.," p. 163); or that "we have the curious and unique case of the mid-style form being more feminine or less masculine in nature than the other two forms" (Ib., p. 257).

With respect to the size of the seeds in the three forms, Darwin says, "There is a gradation parallel to that in the length of the pistil, the long-styled having the largest seeds, the mid-styled the next in size, and the short-styled the smallest" ("F. Fl.," p. 142).

We examined, under a Coddington lens, the size of the seeds taken from the capsules, grown on the river bank, from which the largest produce was obtained. We made five trials of a large number of seeds taken from each set. They were placed before us, at intervals in time, without our knowing to which set the seeds belonged, and every time we ranked them in the following order, which, singularly enough, is exactly the reverse of that given by Darwin. As far as such observation could lead to any definite decision, the order was, short-style seeds largest; mid-style next largest; long-style smallest.

If this is generally the case, then the size of the seeds in that form, which usually is in a very slightly lower position as to the number of seeds, has its power of reproduction possibly equalized with the other two sets; so the long-style, with smaller seeds, has its power equalized with the other sets by the larger number of seeds, which our investigation assigns to it.

This last consideration is, however, of no particular importance, except so far as to show that no superiority as to "feminine" character can be, from such results, assigned to any form.

Darwin, also by his net experiments, came to the conclusion that the pollen of the mid-style form was *less potent* than the pollen of the other two forms.

He compares 13 flowers of the mid-style form, illegitimately fertilized by the *shortest stamens of the long-styled*, with 12 flowers fertilized by *own-form* (that is, "mid-styled") *shortest stamens* (p. 162). The former set produced 47 seeds per capsule; the latter set produced none at all

(Table 24, Divs. III., VI.). Again, he compares 15 flowers of the mid-style form, fertilized by the *longest stamens of the short-styled*, with 12 flowers of the mid-style form fertilized by *own-form longest stamens.* The former set contained an average of 60 seeds; the latter contained an average of 54 seeds (Table 24, Divs. IV., V., p. 155).

These experiments—showing, in Darwin's opinion, the inferiority of the mid-style pollen—he says are corroborated by the legitimate crossings which have already been given, viz., the long-style form legitimately fertilized by the *longest stamens of the mid-style* produced only an average of 51 seeds, but when the same form was legitimately fertilized by the *longest stamens of the short-style*, it produced an average of 107 seeds: and secondly, where the short-styled form fertilized by the *shortest stamens of the mid-styled* produced an average of 64 seeds, and when fertilized by the *shortest stamens of the long-styled* produced an average of 81 seeds.[1]

From these experiments Darwin draws the conclusion, "Hence it is *certain* that the two kinds of pollen produced by the mid-style form are *less potent* than the two similar kinds of pollen produced by the corresponding stamens of the other two forms ("F. Fl.," p. 163. The italics are ours).

Darwin, however, omits to notice a most striking refutation of his theory—viz., that the mid-style pollen was less potent than that of the other two forms—which his own tables supply. In this case (Table 24, Div. V.) 12 flowers of the mid-styled stigma were illegitimately fertilized *by own-form longest stamens* with the result in seeds of:

92, 9, 63, 136, 0, 0, 0, 0, 0, 0, 0, 0.

Four capsules produced together 300 seeds. "Excluding the capsule with 136 seeds," Darwin says, "each capsule

[1] This is given according to the average which Darwin himself draws in his tables, as stated above.

contained an average of 54 seeds, or excluding capsules with less than 20 seeds the average is 77" ("F. Fl.," p. 155). This is a remarkable witness against Darwin's theory of the less potency of the mid-styled pollen in comparison with that of the other two pollens, as all the four cases of "illegitimate unions" of the two other forms of stigma (Table 23, Divs. V., VI., and Table 25, Divs. V., VI.), each with its own-form pollen, are recorded by Darwin as too sterile for any average (pp. 153, 157).[1]

This produce of the mid-style stigma could not have originated from any greater feminine character in the stigma itself which Darwin, as we have seen above, imagined, as we have already seen, from the flowers which were naturally grown, no such character belongs to it.

From this opinion of his, Darwin considered that the defects of the mid-style pollen were made up by the extra capacity of its stigma for fertilization. In his own words, "the mid-style form thus appears to be highly feminine in nature; and although it is impossible to consider its two well-developed sets of stamens which produce an abundance

[1] Darwin says, that he "has hardly a doubt" that the result of the 136 seeds in one of the four capsules recorded above arose from an error of his own when he marked the flower at the time of his fertilizing it. We see no reason, *as far as the number of seeds go*, to doubt the validity of the result given. The flower might have been on a branch which approached nearer to the surface of the net. He expresses himself also in doubt whether a similar error was not committed in respect to the flower mentioned above as producing 92 seeds. "With respect to it," Darwin says, "I do not know what to think" (p. 155, *n.*). In our opinion the two cases confirm the validity of the results in each. This is not the only occasion in which Darwin thinks that he made an error in the experiment, when the result accruing contradicted his theories. We have cited already several instances; it occurs again also in the next Table (Table 25, Div. VI.). Darwin should have arrived at such a conclusion before he counted the seeds, and should have rejected the capsules previously to his doing so, instead of throwing a doubt upon them when he met in the capsules with a produce which contradicted his theory.

of pollen as being in a rudimentary condition, yet we can hardly avoid connecting as balanced the higher efficiency of the female organs of this form with the lesser efficiency and lesser size of its two kinds of pollen grains. The whole case appears to me a very curious one" ("F. Fl.," pp. 163, 164).

Darwin is placed by the natural facts found in plants growing wild recorded above, as gathered by ourselves on October 3rd and 6th, and his own theories on the horns of dilemmas. All three forms gathered at the above dates were growing, at more or less distances, intermixed. If the mid-style pollen is less potent than that of the other two pollens, how is it that the long-styled flowers were superior in their productiveness to the mid-styled, as, if Darwin's theory were correct, they would be exposed, at least in half-measure, to less potent pollen from the mid-style form for their "legitimate" fertilization? And how is it that the mid-style form—which Darwin considered more feminine, and had, according to his theory, the more potent pollen *of both* the other two forms for its "legitimate" fertilization—was yet inferior in its produce to the long-styled form with its less feminine stigma, and which had, in half-measure at least, the inferior pollen of the mid-style to fertilize it? The short-style form also, under the same theory of Darwin, exposed at least in half-measure to the less potent pollen of the mid-style to fertilize its stigma "legitimately," and with a less feminine stigma, was nevertheless equal to the mid-style in productiveness.

We do not wonder that Darwin considered the case, as he imagined it to be, a "curious" one, but the "curiousness" was not in the flowers, but in his fanciful theories, and they arose from Darwin not having more fully examined different sets of wild flowers, and from his being misled by his meeting accidentally with a fully fertile wild spike of the mid-style form alone.

One further reason which Darwin gives in support of his theory of the less potency of the pollen grains of the mid-style form, as quoted above, is "the lesser size of the two kinds of pollen compared with that of the corresponding anthers of the other two forms." "In close connection," Darwin says, "with the lesser potency of the two kinds of pollen of the mid-style form, is the fact that, according to H. Müller, the grains of both are a little less in diameter than the corresponding grains of the other two forms" ("F. Fl.," p. 163).[1]

"It would thus appear," Darwin tells us, "as if the male organs of the mid-styled form, though not as yet rudimentary, were tending in that direction" ("F. Fl.," p. 163). But the cleistogamic flowers teach us that the mere size of the pollen grains has no significance at all as to the productiveness of the pollen on the flowers. "In them"—the cleistogamic flowers—Darwin says, "the degree to which the most important organs have been reduced, is one of their most remarkable peculiarities. In some cases only a single anther is left, and this contains but few pollen grains of *diminished* size" ("F. Fl.," p. 336. The italics are ours). Yet these cleistogamic flowers "produce, as a general rule, quite as many seeds as the perfect flowers" ("F. Fl.," p. 338).

With all the above divergencies and discrepancies, and

[1] The difference in Müller's measurements was only the very minute one of one-half of a division of the micrometer, a division of the micrometer being $\frac{1}{300}$ of a millimetre. Even this very minute difference can hardly be accepted as fully reliable, considering the variability in the flowers; it also might have arisen from an insufficient number of measurements from flowers grown in different situations, for H. Müller says, "The pollen grains differ in size also, according to the length of the stamen that they come from, and there is even a slight difference in size between pollen grains from stamens of the same length, but belonging to flowers of different kinds" ("Fert. of Fl.," p. 257). We do not consider Müller's measurement as in any way a final determination of their comparative size.

with his evident incorrect assumptions that the mid-style form was more feminine than the other two forms, and that the pollen of the same mid-style form was less potent than that of the other two forms, and with the dilemmas on which those assumptions impaled him, we cannot consider that his net experiments give any reliable evidence whatever that there is a special relation between the stigmas and anthers of the same length in these trimorphic flowers of *Lythrum salicaria*.

CHAPTER XXII

TRIMORPHIC FLOWERS

C. Neither a plant of one form of *Lythrum salicaria* grown separately ("F. Fl.," p. 153); nor the barrenness of flowers of the *Lythrum* fertilized under a net with own-form pollen (Table 23, sects. v., vi., p. 153); give Darwin's theory any support.

"In 1863," Darwin says, "I tried a much better experiment. A long-styled flower was grown by itself miles away from any other plant of the same species, so that the flowers could have received only their own two kinds of pollen. *This plant gave an abundant crop of capsules.*[1] *I took by chance* 20 capsules, and they contained an average of 21 seeds per capsule" ("F. Fl.," p. 153. The italics are ours). This plant, being far removed from all other plants of a similar kind, indicates that the locality itself where it was grown was not a naturally selected habitat of the flowers. We have no statement that it was grown on the banks of a river, or in a low, marshy situation, where it would be under the influence of the evening, night, and early morning mists and moisture, at which hours, as we have already seen, the flowers are in their most active condition.

Moreover, the year in which this separated plant was grown (1863), Darwin tells us, was "a very hot and dry season" ("F. Fl.," p. 151); a season most unfavourable to

[1] Compare with this that of a protected plant. "In 1863, a protected long-style plant produced only 5 poor capsules" (p. 145). It was the same year, and so seasons were alike to both plants.

such a plant, especially when out of its own selected habitat. The season was so dry that Darwin tells us that the plants in his own garden "had occasionally to be watered." He says of a plant, on which he experimented in 1863, that "its fertility would perhaps have been still greater had not the summer of 1861 been very hot and certainly unfavourable to some of the plants of Lythrum" ("F. Fl.," p. 200). "*Lythrum salicaria*," Darwin also tells us, "is much affected in its fertility by the nature of the season" ("F. Fl.," p. 189).

Darwin's more general observations on the effect produced on the fertility of plants experimented upon, are especially applicable to *Lythrum* in this case. "It should be observed that the results cannot be considered as fully trustworthy, for the fertility of a plant is a most variable element, depending on its age, nature of the soil, and amount of water given" ("Cr. and S. F.," p. 313).

Nor does Darwin tell us whether this separated plant was raised from seed sown in this locality, or transplanted. That it was either a young plant of the same year, or a transplanted plant, transplanted that year, is to be implied, as far as we can judge, from the context. Darwin's experiments were carried out with these plants in 1862 and 1863 (p. 151). "In 1863," Darwin says, "a long-styled plant *was grown* by itself miles away from any other plant." If a transplanted plant, it would naturally suffer during its first year of being transplanted. If *grown* from seed that year, it could not have become sufficiently aged for its full producing power, as Darwin says of similar plants in his own garden, "I possessed a number of plants in my own garden that, owing to their youth, did not yield a full complement of seed" (p. 143). It might well be the case that from these circumstances combined, the above average of seeds only very partially indicates the self-fertility of a fully aged plant growing in its own selected habitat, and in

an ordinary season. Darwin allows that, "to judge fairly of its fertility, it ought to have been observed during successive seasons" ("F. Fl.," p. 195).

"As these capsules" (on the separated plant) "must have been fertilized by their own two kinds of pollen, and contained a very poor average of seeds," Darwin concludes, "hence insects and chiefly bees act both as general carriers of pollen, and as special carriers of the right sort" ("F. F.," p. 148). But there is one point (besides those which we have already mentioned) connected with Darwin's enumeration of the seeds which much invalidates this conclusion. Not only was the plant under disadvantageous conditions, but, strange to say, Darwin did not adopt, in reference to the capsules, the seeds of which he counted, the same method which he used when he enumerated the seeds in the naturally grown wild plants from which he had calculated the average produce of such plants. When he enumerated the seeds in the wild plants, he tells us that he took "*fine selected*" capsules, but in the case of the separated plant, he says, "*I took them by chance*" (p. 153). As Darwin wished to draw a comparison between the produce of the naturally grown and naturally *crossed* (as he supposed) wild flowers, and flowers naturally *fertilized with their own pollen*, as in the separated plant, it is impossible to comprehend why he should have adopted another method in the latter case from that which he adopted in the former, which nullifies the comparison altogether.

The two best capsules "taken by chance," recorded by Darwin in his enumeration of the seeds produced by this separated plant, contained 35 seeds each, and he calls this its "maximum" (p. 195), whereas he made no effort to select the best capsules (p. 153). To test this average as to what the result would be if we took capsules by chance from a plant naturally grown on a river bank, and in order to avoid all approach to the selection of individual

capsules, we took a single whorl, which was composed of 8 long-styled capsules. The produce of the capsules of this whorl, a whorl taken by chance, was:

15, 94, 24, 54, 8, 84, 11, 71 = 361 seeds; average 45 per capsule.

This whorl—which appeared to us quite equal to any other whorl on the spike excepting the number of capsules on it—was taken from a spike we gathered on the same river bank on which the selected capsules grew, which gave an average in each capsule of 134 seeds. This whorl shows the great irregularity in the produce of the flowers, and how great a difference is made as to the average of seeds in the capsules, when they are *selected*, and when they are merely *taken by chance.*

But even thus—when the capsules are taken by chance—the separated plant of Darwin which, according to his nomenclature, was *illegitimately* fertilized, surpasses in productiveness that of the 13 *legitimately* fertilized flowers of the *same form*—the long-styled flowers fertilized by the longest stamens of the mid-styled. These 13 flowers produced in seeds, as we have already recorded, the following number—

36, 81, 0, 0, 0, 45, 41, 53, 0, 0, 0, 0, 0 = 256 (Darwin's Table 23, Div. i.).

Out of the 20 capsules taken by chance, recorded by Darwin, from the separated plant ("F. F.," p. 153), we give 13, which gave:

20, 25, 35, 21, 26, 24, 23, 30, 27, 29, 20, 29, 35 = 339.

From this comparison one of two results follows, either Darwin's method of experimenting was fundamentally worthless for scientific purposes, or else this *illegitimately* fertilized plant—even with capsules taken by chance, and these from a young plant—was superior in productiveness to one under, what Darwin calls, *legitimate* fertilization.

We are consequently of opinion, from the average

afforded by the separated plant, considering all the disadvantageous circumstances connected with its growth, and the great importance, as seen in our own tables as given above, of the situation in which the plants are grown, that Darwin had no ground whatever for saying that the plant failed in larger produce because there was no pollen near of the right sort, which the bees could convey to the flowers; nor any proof from this instance—from its comparative failure to produce in capsules "taken by chance" a larger number of seeds—that "insects and *chiefly bees* act as general carriers of pollen, and as *special carriers* of the *right sort*" (p. 148. The italics are ours).

This separated plant affords also another striking evidence of the unreliable character of Darwin's net experiments, and of the sterilizing effect which the net produced. This long-styled separated plant, fertilized with its "own pollen"—with all the disadvantages connected with it—"produced an abundant crop of capsules" (p. 153), and the two best capsules of those which he took by chance gave a product, as we have stated, of 35 seeds each.

When we look to Darwin's experiments (Table 23, Divs. V., VI., p. 153), 15 flowers of the *long-styled plant*, fertilized by own-form pollen of its own mid-length stamens, and by own-form pollen of its shortest stamens, the following was the result, in seeds, in each case respectively:

2, 10, 23, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0,
4, 8, 4, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.

Thus 15 flowers, under the net, produced in one case *only 35 seeds altogether, and only* 16 *seeds in the other case*, and in each case there were 12 perfectly barren flowers. Such was the result though the pollen applied to these flowers under the net was, as far as its *form* was concerned, exactly the same as that which was necessarily furnished to the flowers of the separated plant.

Such a result, even if it stood alone, is ample evidence

that Darwin's net experiments give no reliable or natural result.[1]

The above is not the only case of a long-styled plant of *Lythrum*, when fertilized by own-form pollen, proving the utter invalidity of Darwin's tabulated net experiments with own-form pollen.

A long-styled plant, growing with 18 other long-styled plants "which flowered by themselves, and thus were illegitimately fertilized with own-form pollen" (pp. 195, 196), produced from 10 capsules an average of 71 seeds. (In the Tables just above, as we have seen, 30 flowers, similarly fertilized, produced altogether only 51 seeds.) On this result Darwin remarks, "The average is so remarkably high that I cannot understand it." In fact, he would not understand it; it contradicted his theory. It was Nature asserting herself. It seems that the flowers, either from the character of the weather when the flowers were in bloom, or from their position under the net, or some other circumstance, overcame the sterilizing influence of the net and displayed an approach to the natural fertility of flowers growing wild.

It is quite unnecessary to give any further instances of Darwin's net experiments with *Lythrum salicaria*. The above cases show sufficiently their invalidity.

In all the tabulated cases which Darwin records (the chief of which we have given above), only pollen from one set of stamens was applied in each experiment. He was under the impression that no more seed was produced by the two kinds of pollen than by "one kind by itself" (p. 164). To this opinion the experiment with the flower

[1] We are surprised that Darwin did not continue to observe the results in this plant during successive years, as he says himself, as quoted above, that to judge fairly of its produce it should have been so observed. More especially is this our opinion, as he considered this method a much "better way" of experimenting (p. 153).

"grown miles away from all others" doubtlessly led him. This might be perfectly true when Darwin happened to hit on the exact time at which both stigma and the pollen were in their maturest form when he applied the latter. By such a happy chance he might occasionally, as he did ("F. Fl.," p. 164), find a few capsules which produced as many seeds, or even more, than the wild ones. But in such cases we may recall what Professor G. Henslow says, "that plants are never so carefully crossed in Nature, as was the case in Darwin's experiments, where the unalloyed influence of crossing brought about a much more enhanced stimulus than ever occurs in the wild state." "Floral Structures," p. 317.

The natural provision of two sets of stamens of different lengths in each of those flowers necessarily suggests that this arrangement is closely associated with the economy of the flowers.

This provision indicates some peculiarity in the relation of the two sets of stamens to their respective stigmas. What that peculiarity may be there is as yet no direct indication; at least none has as yet been definitely discovered.

The two sets of stamens being very differently proportioned, and so possibly arriving in some seasons, or in every season, at maturity at very slightly different hours of the night or day, should have led Darwin to the very natural inference that it was absolutely necessary that the application of the pollen of both sets of stamens should be possible *during the whole time, from the commencement of the maturity of the one set to the close of the maturity of both*, if a natural result was to be obtained. It is impossible for any observer, as Darwin himself allows, to tell exactly when the stigma of any flower is in its most receptive state ("Cr. and S. F.," p. 23), or the pollen in its most mature condition.

The *Lythrum* being also a waterside plant, it was, as

we have seen, particularly influenced by the rising of evening damp or mists, or morning dew or moisture. Darwin does not tell us that he made any experiments of fertilizing the flowers at the latest hours of the evening, or at the earliest hours of the morning.

The necessity of such conditions being fulfilled is shown by Darwin's own observations. "All who have crossed plants," Darwin says, "know that *successive applications* of pollen, on the most favourable days and at the *most favourable hours*, highly favour fertilization" ("F. Fl.," p. 153. The italics are ours). He says of the so-called illegitimate unions, which were sterile in his experiments, that "if such unions were to be effected *repeatedly* by the aid of insects, under the most favourable conditions, some few seeds would be produced in every case" ("F. Fl.," p. 164).[1]

Unless Darwin's experiments were carried out during the most propitious hours, from about 8 p.m. to 8 a.m. (as we have seen in our previous chapter), about which he says nothing, it might well account for the large number of unfertilized flowers found amongst the cases of "own-form" pollen fertilization, where the pollen in some cases, if not in all, had already been weakened by being developed under a net.

Though Darwin in his tabulated experiments did not use both kinds of pollen, yet he did practise such experiments, though seemingly in a very partial manner. He says, in connection with his tabulated experiments, "Besides the above experiments, I fertilized a *considerable number* of long-styled flowers with pollen taken by a camel's hair brush, from both the mid-length and shortest stamens of

[1] Such repeated application does not seem to have been practised in his experiments with *own-form pollen*, as recorded above, as out of 74 flowers, which were tabulated as experimented upon (pp. 153, 155, 157), 61 of these flowers, so fertilized, produced not a single good seed.

their own form; only 5 capsules were produced, and these yielded on an average 14 seeds" (p. 153).

Similarly carried out experiments were made with a *considerable number* of the mid-styled form, and the result was very much the same as with the long-styled, "5 capsules were produced, and these yielded an average of 11 seeds."

Of the short-styled form of these experiments, Darwin says, "I fertilized a number of flowers without particular care with their own two kinds of pollen, but they did not produce a single capsule" (p. 157).

Such were the meagre results which Darwin obtained when he experimented—in one case without any particular care at all—with the two kinds of pollen. The results were such as might have been anticipated. He seems not in any way to have carried out with them the conditions which were absolutely necessary for valid and reliable results. Without such conditions being fulfilled, viz. possibility of continuous application of pollen, and that at the most favourable hours, and in the most favourable situations, and from both sets of stamens during the entire period of their maturity, no experiments with such flowers could be relied upon as giving a true interpretation of the fertility, which each flower with its own stamens naturally possessed.

Evidently, from the examples above, neither the separated plant, nor the negative evidence of the flowers being barren with their own pollen *under the net*, give any support to Darwin's theory that there is a special relation between stamens and stigmas of the same length in trimorphic flowers.

CHAPTER XXIII

TRIMORPHIC FLOWERS

D. The cleistogamic flowers directly disprove the theory.

What, however, Darwin did not do, and to carry out which, artificially, there would be almost insuperable difficulties, Nature has herself, in her own adaptation, effected. Nature has solved the question for us by her own natural act. In the case of one trimorphic plant we have unexceptional evidence that no intercrossing is needed for perfect fertility in these trimorphic flowers. This evidence is afforded by *Oxalis sensitiva.* This is the only heterostyled trimorphic plant that is as yet known to produce cleistogamic flowers ("F. Fl.," p. 340). These cleistogamic flowers never open. "They are invariably self-fertilized," Darwin says, "yet they produce an abundance of seed" ("F. Fl.," p. 311).[1]

[1] Cleistogamic, or closed flowers, grow upon the same plants as the open flowers. These closed flowers are very inconspicuous—they are more like buds than flowers; the petals are usually merely minute scales; they are consequently often quite overlooked by a great number of botanists. They are to be found on several English plants, but are particularly to be met with on the Dog Violet and in smaller numbers on the Sweet Violet, on the Wood Sorrel (*Oxalis acetosella*), on a few of the Vetches and the Subterranean Clover (*Trifolium subterra- cum*), and on many others. In the Dog Violet they appear occasionally, together with, but usually some little time after, the open flowers. In other plants they show themselves sometimes before, sometimes after, and occasionally simultaneously with the open flowers.

Now, by Darwin's theory, as we have seen, no heterostyled trimorphic plants could produce flowers perfectly fertile, unless the pollen from another plant of a different form was brought to its flowers from stamens in those flowers of corresponding length with its stigma.

But in *Oxalis sensitiva*, "the long-styled cleistogamic flowers are produced by long-styled plants; the mid-styled as well as the short-styled cleistogamic flowers are produced respectively by the other two forms; so that there are three kinds of cleistogamic, and three kinds of perfect flowers produced by this one species" ("F. Fl.," p. 323). Now, as Darwin, from his *net experiments*, concluded that "most of the heterostyled species of *Oxalis* are more or less sterile, many absolutely so, if illegitimately fertilized with their own form pollen" ("F. Fl.," p. 323), he had in some way to account for this extreme contradiction in results between the naturally abundant fertility of these cleistogamic flowers, and his own results, which we have given above, of *Lythrum salicaria*, under the unnatural method of experimenting with his net. Under this difficulty, Darwin suggests, "it is probable that the pollen of the cleistogamic flowers has been *modified* in power, so as to act on their stigmas, for they yield an abundance of seed" ("F. Fl.," p. 323. The italics are ours).[1]

That the pollen of the closed flowers should be different in power from that of the open flowers on the same stem, and from the same root, is merely a gratuitous assumption. This assumption might have some possible validity, if seeds

[1] Darwin makes the same assumption concerning an equal-styled form of *Primula auricula*, that it "was *modified* in some special manner, not only in structure but in functional powers" ("F. Fl.," p. 223), because the results produced in seeds contravened his theory. The same assumption is made concerning *P. veris* and *P. sinensis* ("F. Fl.," p. 273), as their results also were contradictory to his opinions; so again of *Lysimachia vulgaris*, *Viola tricolor*, and other flowers ("F. Fl.," p. 4).

from cleistogamic flowers alone produced the plants on which the cleistogamic flowers grew. But that is not the case. The seeds from the open flowers produce not only plants bearing open flowers again, but bearing cleistogamic flowers as well. There can be no different power in the pollen of the cleistogamic flowers generally than that which is naturally possessed by the pollen of the open flowers, from whose fertilization those seeds which produce the cleistogamic flowers sprung. Many flowers, moreover, which are not cleistogamic, are fertilized in the bud before the flower opens, yet no one could suppose that the pollen of the unopened buds was *modified, or different in power* from that of the open flowers. In fact, this very flower, *Oxalis sensitiva*, produced these unopened buds also. "Many of the early flowers," Darwin says, "on a mid-styled plant in my hothouse, did not open properly, and were in an intermediate condition between cleistogamic and perfect; nevertheless, they produced capsules" ("F. Fl.," p. 332). "I am far from wishing to assert," Darwin says (speaking generally of fertilization), "that some flowers, during certain seasons, are not fertilized in the bud, for I have reason to believe that this is the case" ("F. Fl.," p. 98). There can be no general ground whatever for inferring that on the same plant, with the same food, temperature, light, and moisture, the pollen of cleistogamic flowers is different in power from that of flowers in the bud, or that pollen of flowers in the bud differs from that in the open flowers. The results, according to Darwin's testimony, are the same. "The seeds produced by the cleistogamic and perfect flowers do not differ in appearance or number" ("F. Fl.," p. 316). For Darwin to suggest that a covering provided by *Nature* modifies the pollen, and that his own net gave a *natural* result, is more than one can reasonably be expected to accept.

From these cleistogamic flowers we obtain the key to the interpretation of the fertilization of these flowers. From them we learn that the pollen of each flower is the natural provision for the fertilization of that flower; that this is the ordinary rule, subject to more or less cross-fertilization in the open flowers. These cleistogamic flowers, with "their abundance of seeds" ("F. Fl.," p. 329), consequently, quite do away with the statement of Darwin, that "two of the three forms must co-exist, and the pollen must be carried by insects reciprocally from one form to the other, in order that either of the two should be fully fertile" ("F. Fl.," pp. 138, 345). In fact, they do away generally with the very whimsical notion of Darwin about the fertilization of trimorphic plants. Nature herself contradicts in these cleistogamic flowers the theory of Darwin, and Natural Science generally has accepted for its motto—

Nunquam aliud Natura, aliud sapientia dicit.

The last argument which Darwin calls up as favouring his views concerning the fertilization of these trimorphic flowers is based upon his own erroneous views concerning the two forms of *Primula.* "From the dusted condition of the bodies of the bees which I caught on the flowers," Darwin says, "it is probable that pollen of various kinds is often deposited on all three stigmas, but from the facts already given with respect to the two forms of *Primula*, there can hardly be a doubt that pollen from the stamens of corresponding length placed on the stigma would be prepotent over any other kind of pollen, and obliterate its effects" ("F. Fl.," p. 164).[1]

The Primrose (*P. vulgaris*), as we have already seen, gives no support whatever to the idea that the pollen of any

[1] The case of the short-styled, dark Polyanthus (here particularly, we suppose, alluded to by Darwin), which occurs in "Forms of Flowers," p. 31, has been already mentioned in Chap. XI., and shown to give no reliable evidence whatever to such a supposition.

other form is more potent on its flowers than that of their own pollen. So far from this being the case, the primrose, in the short-styled form contravenes it by being actually self-fertilized, and also the most productive of the two forms.

Even if the results of Darwin's experiments were not explicitly contradicted by the cleistogamic flowers, we cannot see how Darwin, in such a complicated theory which he formulated, could have expected his results to be accepted as absolutely reliable, even if his method was reliable, as his results were tabulated from a very insufficient number of trials. He says, "It would have been advisable to have repeated each of the eighteen unions a score of times." The wonder is not that Darwin did not make more experiments, but that he had the marvellous patience to carry out on these flowers the experiments that he did. He truly says that to have done more "the labours would have been too great" ("F. Fl.," p. 150).[1]

We are consequently, from all the above considerations, very far indeed from accepting Lord Avebury's statement. "Mr. Darwin has proved by experiments that the species of *Lythrum salicaria* does not set its seeds if the visits of insects are prevented" ("Fl. and Ins.," p. 102). Still less can we accept Mr. Wallace's more absolute dictum. "There is the clearest proof" (!) "that these complex arrangements (in trimorphic flowers) have the important end of securing a more abundant and more vigorous offspring" ("Nat. Select.," p. 466). "A phenomenon," Mr. Wallace adds, "which, if it were not so clearly established, would have appeared in the highest degree improbable" ("Darwinism," p. 311).

[1] Kerner tells us that *Silene nutans* (which is also an English flower) is "very remarkable as producing tetramorphic flowers" ("Flowers and their Unbidden Guests," p. 134, *n.*). We cannot surely suppose that in such a flower there are all these special limitations to full fertility which Darwin supposes to be the case with the dimorphic and trimorphic flowers.

It seems to us almost inexplicable that Darwin, when he wished to compare the natural productiveness of self- and cross-fertilization, did not avail himself of those instances which were *naturally* afforded him. All plants which produce both cleistogamic and open flowers supplied him with specimens by which such a comparison might be attained. Instead of accepting Nature's net in those plants which provided them in abundance, as in the *Leguminosæ*, and other plants, he substituted a net of his own construction. Every naturalist would assuredly allow that flowers, in which cross-fertilization was *naturally* prevented, afforded more reliable evidence as to self-fertilization than flowers subjected to the unnatural method adopted by Darwin in his test experiments. The only reason that we can suppose for Darwin ignoring the evidence of the cleistogamic flowers in such a comparison was that they in every case equalled, and in some cases surpassed, in fertility, the open flowers on the same plant. They thus contradicted the theory of Darwin that "self-fertilization is often injurious" ("Cr. and S. F.," p. 439); and that "the difference between the self-fertilized and cross-fertilized raised by me is due to the injurious effects of self-fertilization" (Ib., p. 440).

CHAPTER XXIV

VARIATION IN THE LENGTH OF THE STYLES IN PRIMULACEÆ A "POSITIONAL," NOT A "FUNCTIONAL," VARIATION

In our examination of very considerably over 500 flowers of the *long-styled form of primrose*, each gathered from a different root, we found styles of every variety of length; some exceeding the length of the corolla tube; some equal to the corolla tube; others halfway down between the mouth of the tube and the anthers below, eight shortened styles touching the tops of the anthers with the base of their stigmas; and two stigmas enclosed in the midst of their anthers placed in the middle of the corolla tube, with the top of their stigmas visible and exactly on a level with the top of the anthers. In these two cases, both the stigmas and the ovaria were perfectly healthy.[1]

There was no appreciable difference, as far as we could

[1] In 34 other instances we found the stigmas involved in the midst of the anthers, and invisible; but in these cases both the styles and ovaria were discoloured and unhealthy, the latter—the ovaria—wrinkled and dark coloured. The stigmas in these cases seem to have been arrested in their progression towards the mouth of the corolla by the anthers—which, as we have pointed out above, curve inwardly towards the centre of the corolla tube—for their styles were generally bent and distorted. These cases occurred in the month of March and in the earliest days of April, when, perhaps, the frosty nights had affected and weakened the styles, and they were consequently unable to force the stigmas through the anthers. We also found a few unhealthy stigmas below the anthers placed in the middle of the corolla tube, with their ovaries also unhealthy.

observe, under a Coddington lens, in the stigmas of these two flowers as to smoothness from that found in the short-styled stigmas.

In our examination also of very considerably over 500 specimens of the *short-styled form of primrose* gathered from different roots, every variation in length of styles was found, from in one case an almost sessile stigma to 10 instances in which the stigmas touched the base or centre of the anthers at the mouth of the corolla.

Darwin mentions, as occurring in the Cowslip (*Primula veris*), instances of a similar kind to those 10 last mentioned, which we found occurring in the primrose. These instances occur under the heading "Equal-styled varieties" ("F. Fl.," p. 273). He says, "In the case of *P. veris*, the stamens resemble in length, position, and size of their pollen grains, the stamens of the short-styled form; whilst the pistil closely resembles that of the long-styled, but as it varies much in length, *one proper to the short-styled form* appears to have been elongated, and to *have assumed at the same time the functions of the long-styled pistil*. Consequently the flowers are capable of spontaneous fertilization of a legitimate kind" (in Darwin's nomenclature) "and yield a full complement of seed, and even more than the number produced by ordinary flowers legitimately fertilized" ("F. Fl.," pp. 272, 273. The italics are ours).

In those 10 elongated pistils of the short-styled form of *primrose* which we found, no change as to the papillose character of the stigmas was perceptible—nor does Darwin notice any alteration in his case in this respect in the cowslip, as he says, "One *proper* to the short-styled form appears to have been elongated"—when thus touching the base of the anthers, as even the stigmas were still closely covered in by the incurved apices of the anthers. Their structures would be slightly, if at all, affected in such altered position by any atmospheric influence.

Now, it is perfectly obvious that in these instances of *P. veris*, mentioned by Darwin, the cases were those of the stigmas of the short-style elongated as in the 10 instances mentioned above in the *primrose.*

Darwin, in order to reconcile his theory of the necessity of cross-fertilization in the cowslip with the fact connected with these flowers that "they yielded a full complement of seed, or even more than the number of ordinary flowers legitimately fertilized," accounts for it by saying that the short-styled form appears to have been elongated, and "to have *assumed* at the same time the *functions* of the long-styled pistil" ("F. Fl.," p. 273). But these flowers, from the position of the anthers, were evidently short-styled ones with the pistil elongated; and there was in reality no assumption whatever by them of any function but that which was *inherent* in the short-style form itself.

We have already seen how Darwin, because it contradicted his theories, suggests that the pollen of the cleistogamous flowers in *Oxalis sensitiva* was "modified." This is a similar case, in which Darwin, instead of allowing that his theory was in fault, attributes a *change in function* to a mere change in length of pistil. Moreover, in the comparison which he draws between the fertility of these flowers and the fertility of his own "legitimately" fertilized ones, Darwin assumes that what he calls "legitimate" fertilization is the natural fertilization of these flowers. This we have already seen to be contrary to the facts connected with them.

In these last instances of equal-styled *Primula vulgaris* and *P. veris*, the stamens and pistils are at the mouth of the corolla. In the instance which we now give the position is reversed. This instance is that of *Primula sinensis*, where both the stamens and the pistil are halfway down the corolla.

"The stamens," Darwin says, "resemble in all respects

the shorter ones proper to the long-styled form, whilst the pistil makes a near approach to that of the short-styled, but as it varies in length, it appears as if a long-styled pistil had been reduced in length, and *modified in function*. The flowers in this case, as in *P. veris*, are capable of spontaneous legitimate fertilization, and are rather more productive than ordinary flowers legitimately fertilized" ("F. Fl.," p. 273. The italics are ours).

That the above instance was nothing more than a long-style lowered is evident from a similar instance given by Darwin of an equal-styled variety of the same plant (*P. sinensis*). "This flower was a *long-styled plant*, descended from a self-fertilized long-styled parent, which had some of its flowers in an anomalous state, namely, with the stamens placed low down in the corolla, as in the ordinary long-styled form, but with the pistil so short that the stigmas stood on a level with the anthers. These stigmas were nearly as globular and *smooth as in the short-styled form, instead of being elongated and rough as in the long-styled form*" ("F. Fl.," p. 218. The italics are ours). This is the more noticeable in *P. sinensis*, as Darwin, in his description of the stigmas of the flower, says, "The stigma is considerably rougher than that of the short-styled" ("F. Fl.," p. 38). "But the structure varied," Darwin continues, "much even on the same umbel; for in two flowers the pistil was intermediate in length between that of the long-styled and that of the short-styled form, with the stigma elongated as in the former and *smooth as in the latter*; and in three other flowers the structure was in all respects like that of the long-styled form. These *modifications* appeared to me so remarkable that I fertilized eight of the flowers with their own pollen, and they became abnormally fertile in comparison with those of ordinary long-styled plants when self-fertilized" ("F. Fl.," p. 218. The italics are ours).

In this last case of *P. sinensis*, we have a graduated change from the long-styled to the equal-styled form on the same plant, and even on the same umbel, yet even this case is cited by Darwin, under "*Equal-styled variety of P. sinensis*," on account of their abundant fertility, as an example of "a variation in structure combined with *changed function*" ("F. Fl.," p. 218); "so that a self-union in the case of the equal-styled variety is, in fact, a legitimate union" (p. 220)!

A change in function of some of the pistils of the flowers, not only on the same plant, but on the same umbel, whilst other flowers remained unchanged in structure, and so we suppose, in Darwin's opinion, also in function,[1] seems to us to accord two natures to the pistils on the same plant and on the same umbel, and so to be utterly unnatural. If such, however, were the case, we might reasonably ask at what stage in the transition did the change in function take place? The average difference in length between the short- and the long-styled pistils is, we may roughly say, in the Primulaceæ, from 3 to 4 millimetres. Did the change in function in the pistil begin when it started on its shortening journey as it changed to an equal-styled flower? or did it begin when there were only 3, or 2, or 1, millimetres difference in length from its corresponding anthers? or did it not take place until the entire difference was obliterated, and it had become truly equal-styled?

The inherent nature or function in these pistils remained, in our opinion, the same as in the other sets of flowers on the same plant, and was not changed during the pistil's course of shortening. In this change it was merely a positional (so common in the *Primulaceæ*), not a functional change. The increased fertility of the flowers arose, as we

[1] By Darwin's use of the term "these *modifications*"—as quoted above—we imply that he limited his test to the modified flowers alone.

might reasonably suppose—and as even Mr. Scott suggests to Darwin, as one of the causes in the similar case of the red variety of *P. veris*—from the close approximation of the stigmas and anthers in the flower itself ("F. Fl.," p. 235). Nor need Darwin have been surprised that the eight flowers which he *fertilized* became "abnormally fertile" in comparison with ordinary long-styled flowers *self-fertilized under the net.*[1]

In like manner peculiarly exceptional variations were met with by Darwin and Mr. Scott in the case of some flowers of *P. auricula*—two by Darwin and five by Mr. Scott —in which the anthers and pistils were at the mouth of the corolla, and the pollen grains resembled in their small size those of the shorter stamens of the long-styled form; their stigmas also were of the same long-styled form. When Darwin found that one of the flowers, when self-fertilized, produced a greater quantity of seed than he expected from an equal-styled flower, in which both pollen grains and pistils were of the same form, he came to the conclusion that "the male and female organs of this equal-styled variety had been *modified in some special manner, not only in structure, but in functional powers*" ("F. Fl.," p. 223. The italics are ours).

This flower, though thus productive beyond Darwin's expectation, was, he says, "far inferior in fertility to either form when legitimately crossed" ("F. Fl.," p. 223). But such a

[1] The view that the increased fertility of these flowers arose merely from the close approximation of the anthers and stigmas is supported by the abundant fertility of those species of *Primula*, which, as Darwin says, "are homo-styled: that is, they exist only under a single form. On such Primulas as *P. scotica, mollis*, and *verticillata*, Mr. Scott experimented and found these flowers yielded an abundance of seeds when fertilized by their own pollen" ("F. Fl.," p. 50). In those flowers of the primrose which we have met with, where the short-styled stigma was elongated until it touched the base of the anthers, and so became equal-styled, the stigma was, when the pollen was ripe, loaded with pollen.

result is what might naturally be expected. These crossed plants were fertilized by naturally grown pollen, and very efficiently fertilized by the direct application of it; but the self-fertilized was under a net, and so it was imperfectly fertilized by being deprived of the full action of the wind to shake the pollen, and the latter itself would be imperfectly developed and matured under a net.[1]

Other instances might be given where the pistils varied in length, and the stigmas in shape, even on the same plant, as in *Primula rubra* ("F. Fl.," p. 225), but we think that we have instanced a sufficient number.

It is strange to what conclusions Darwin was driven by the exigencies of his theory. Changes in the function of the pistil, or in the function of the anthers, or in both, in these flowers must be assumed in order to reconcile his theory—that the two forms were sexually distinct—with the facts connected with them as to fertility. Here facts were presented to him which distinctly contradicted his theory. If Darwin had only observed, which he unfortunately failed to do, that the short-styled Primrose, when growing naturally, was not subject to cross-fertilization, and yet was fully productive, he would have seen at once, when the stigma was lengthened to an equal-styled condition

[1] In the equal-styled flowers, *P. auricula* and *P. farinosa*, the anthers and stigmas are at the mouth of the corolla, and their pollen grains, Darwin tells us, resembled in their small size those of the short stamens of the long-styled form; the stigmas were of the same form. The flowers of the two Primulas were consequently exactly similar as to form in their pollen grains and stigmas—both long-styled forms—yet under Darwin's experiments the flowers of the one—*auricula*—were amply "fertile with their own pollen," and the flowers of the other—*farinosa*—were "extremely sterile with theirs" ("F. Fl.," pp. 223, 224). Such results show not only the utter unreliability of such *net experiments*, but also that no confidence can be placed in any assumption that modification has taken place in the function of pollen or stigma, as here we have, under similar conditions, the fertility of the flowers of one Primula, and the sterility of its kindred Primula.

without any sensible change in productiveness, that such variation was merely a "positional," not a "functional" variation, and that it would be a violation of all analogy to give a different interpretation to the shortening or lowering of the pistil in the long-styled form of the same species, especially in the case of the *Primulaceæ*, where every variety was found in the pistils of both forms. Still more would this be the case, when upon the same long-styled plant, and on the same umbel, "some stigmas stood on a level with the anthers; others were intermediate in length between that of the long- and that of the short-style form; and in other flowers the structure was in all respects like that of the long-style form."

We consequently can draw no other conclusion from the facts which have been produced in the preceding pages, than that the length of the styles, or the roughness and smoothness of the stigmas, is a "positional," not "functional" variation.

CHAPTER XXV

VARIATION IN SIZE OF THE POLLEN GRAINS A "POSITIONAL," NOT "FUNCTIONAL," VARIATION

The minute difference in the size of the pollen grains of the two forms of heterostyled flowers is discovered, Darwin tells us, when examined under a microscope ("F. Fl.," p. 16). It is not a characteristic of all heterostyled flowers, but in all the species where it does exist, with only one or two exceptions, and those cultivated flowers, as far as we are aware, the smaller pollen grains are always found in the anthers of the long-styled flowers, and the larger pollen grains in those of the short-styled ones. This characteristic is found generally in the *Primulaceæ*. Lord Avebury considers that this difference is one of particular importance. "The importance of this difference," Lord Avebury says, "is probably due to the fact that each grain has to give rise to a tube which penetrates the whole length of the style, and the tube which penetrates the long-styled stigma must, therefore, be nearly twice as long as in the other" ("Fl. and Ins.," p. 40). This opinion is, of course, based on the supposition that cross-fertilization takes place from the short-styled anthers to the long-styled stigmas, and *vice versâ* from the long-styled anthers to the short-styled stigmas. It consequently subserves the opinion of the cross-fertilization of heterostyled flowers.[1] But

[1] H. Müller, speaking of heterostyled plants, falls into the same error, saying, "The size of the pollen grains is always proportional to the length of the style that its tube has to traverse" ("Fert. of Fl.," p. 10).

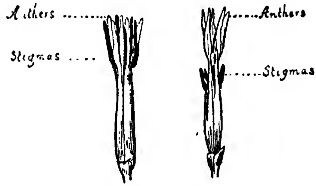
Darwin gives no support to such an idea, as that which Lord Avebury propounds. Darwin, from the case of *Linum*, and of other flowers, says, "These cases seem to prove that the difference in size between the grains of the two forms is not determined by the length of the pistils down which the tube of the pollen grains have to grow; that with plants in general there is no close relationship between the size of the pollen grains and the length of the pistil is manifest" ("F. Fl.," p. 250). Darwin then gives instances in the cases of Limnanthemum and Coccocypselum as proofs of his opinion ("F. Fl.," p. 250). The short-styled Primrose absolutely refutes the idea. In that flower, as we have seen above, the stamens, with the larger pollen grains, form a kind of closed box overhanging the pistil, and opening within into the corolla tube, drop their *larger* pollen grains on the *shortest* form of stigma, and these flowers are fully productive. We cannot conceive, after such an instance, that such an assumption has any ground of support at all.

May not this minute difference in size and shape in the grains of the two forms be attributable merely to the fact that the stamens with the larger pollen grains are found in the short-styled form, where they are from their position at the mouth of the corolla tube fully exposed, in contrast to the other form, to the sun and all other atmospheric influences?

Nor is this view without strong confirmatory support. In the Cowslip (*Primula veris*) the grains of the short-styled form are, according to Darwin, in diameter to those of the long-styled as 100 to 67 ("F. Fl.," p. 16), and in the primrose as 100 to 71 (p. 36); whereas in *Pulmonaria angustifolia* (one of the Boragineæ), which has a much more open corolla, almost as open as that of our common wild Harebell (*Campanula rotundifolia*), in which any difference in atmospheric influence would be much reduced, "the average diameter of the short-styled pollen grains is to that

of the long-styled only as 100 to 91" ("F. Fl.," p. 106); whilst in *Linum grandiflorum*, in which the stamens of both forms are fully exposed to the atmosphere at the top of the corolla, "the foliage, corolla, stamens, and pollen grains," Darwin says, "are alike in the two forms; the difference is confined to the pistil" ("F. Fl.," p. 81).

In the accompanying diagram, Fig. 23, of *Linum grandiflorum*, which is after Darwin ("F. Fl.," p. 82), the position of the stamens is shown. In the short-styled form



Long-styled form   Short-styled form
of *Linum Grandiflorum* (Crimson Flax).

FIG. 23.—In the long-styled form both the stamens and stigmas are outside the corolla. In the short-styled form the stigmas are within the corolla.

the stigmas lie within the tube of the corolla; in the long-styled they are without the tube. In both forms the anthers are without the corolla tube ("F. Fl.," p. 82).

The same occurs in *Cordia*, of which Darwin says, "The anthers of both forms are situated in the mouth of the corolla. I could not detect any difference in the size of their pollen grains" ("F. Fl.," p. 118).

Exactly the same occurrence was met with in *Phlox subulata* as in *Cordia*, where "the anthers in both forms hold a similar position at the mouth of the corolla." [1]

The same difference in the size of the pollen grains, according to their relative length and exposure, is usually

[1] Darwin expresses some doubt as to *Phlox subulata* being truly heterostyled ("F. Fl.," p. 120).

found in the trimorphic flowers. In *Lythrum salicaria* "the pollen grains varied in their diameter, according to the division of the micrometer,"

from $10\frac{1}{2}$, in the case of the longest stamens of the short-styled form,

to 6, in the shortest stamens of the long-styled.

The same was also found to be the case in the trimorphic heterostyled *Oxalis valdesiana*. "We here see," Darwin says, "that the largest pollen grains come from the longest stamens, and the least from the shortest" ("F. Fl.," p. 143).

That the difference of position of the anthers, combined with difference in exposure to atmospheric influences, may account for the difference in the size of the pollen grains of the dimorphic flowers of the *Primulaceæ*, without involving any functional difference, is also, in addition to the facts already given in reference to these flowers, very strongly supported from the two forms in the *Primulaceæ* being, as we shall see below, nothing more than mere, though, in some of the species, very persistent, varieties.

We have already seen, under the trimorphic flower (*Lythrum salicaria*), that Darwin's idea of a special function, being attached to a special length of stamen, is unsubstantiated by his various experiments, whether under the net or in the open fields. The variation in size of the pollen grains in these cases, and with strong evidence in their case, as in the case of the *Primulaceæ*, that the three forms, as we shall see subsequently, are mere varieties, and with no evidence of a contrary tenor, must consequently be similarly considered as only a "positional," not a "functional," variation.[1]

[1] In a species of *Pontederia*, "an aquatic plant, which is allied to the *Liliaceæ*, and which grows in the greatest profusion on the banks of a river in Southern Brazil" ("F. Fl.," p. 183), there are in the flowers the two forms of stigma, the long-styled and the short-styled; below the former are two sets of stamens of different length; above

the latter there are also two sets of different length, just as in the long-styled and short-styled forms of the trimorphic plant *Lythrum salicaria* (Fig. 19). In Pontederia, however, the mid-style form, corresponding in the position of its style to the mid-anthers of the two other forms in Pontederia, has never yet been found. "Fritz Müller," Darwin says, "although he examined a vast number of plants, could never find one belonging to the mid-style form" (p. 183). In the absence of a mid-style form, if such middle stamens were "functional," according to Darwin's idea, they would also in this case be perfectly purposeless. We can scarcely saddle, by accepting Darwin's theory, such purposelessness upon Nature.

CHAPTER XXVI

TRANSPARENCY AND FORMS OF POLLEN GRAINS, AND THE RELATIVE TIME OF THE TWO FORMS OF THE FLOWERS APPEARING

THERE are three other smaller differences in these flowers which Darwin instances, but which we only incidentally notice, as they are very unimportant differences. These are the form, and the transparency, of the pollen grains, and the time at which the two forms relatively to each other appear in bloom.

Darwin tells us that the two sets of pollen grains differ in shape, as well as in size, "the grains from the short-styled being nearly spherical, those from the long-styled being oblong with angles rounded" ("F. Fl.," p. 16). This difference cannot be of any importance, much less of any functional importance, as Darwin says, "but the difference disappears when the grains are extended with water" (Ib.).

Darwin also notices that the smaller grains of the long-styled are more transparent than the larger grains of the short-styled, and apparently in a greater degree than can be accounted for by their less diameter" ("F. Fl.," p. 16). The greater transparency was caused, doubtlessly—in contrast to the more exposed grains of the short-styled—by their being covered up in the lengthened tube of their corolla, as it is just the same with the "pollen grains" of

the cleistogamic flowers "which have remarkably transparent coats" ("F. Fl.," p. 310). These latter flowers are not affected functionally at all by their transparency. The condition of the two sets—one covered by its lengthened corolla (the long-styled pollen of the Primula), and the other by its unopened corolla (the cleistogamic pollen)—is closely analogous, and would consequently tend to bring about similar results as to transparency.

The third difference which Darwin mentions is, that "the long-styled generally tend to flower a little before the short-styled. For instance," Darwin says, "I had 12 plants of each form, growing in separate pots and treated in every respect alike; and at the time when only a single short-styled plant was in flower, seven of the long-styled had expanded their flowers" ("F. Fl.," p. 16). This is, of course, a very limited observation indeed, from which to conclude the tendency as to the relative time in which the different forms flower. The precedence of the one over the other might easily, in such a case, have been purely accidental. Our own experience, from the wild plants of the Primrose, does not accord with Darwin's conclusion drawn from these very limited instances of cultivated Cowslips.

In one year we gathered from separate roots in every kind of situation, and we took them as they came—

In March	541	long-styled	511	short-styled
In April	552	"	498	"
In May	172	"	150	"
	1265	"	1159	"

making altogether a total of 2424 flowers; so that the long-styled exceeded the short-styled in number by 106. It is noticeable that in March, in which month we gathered the *earliest* flowers that appeared in different localities, the

proportion of long-styled to short-styled is less in the excess of the former over the latter than it is in the later months. There is, therefore, from the above comparison as to the time of flowering, no indication of any functional difference between the two forms.[1]

[1] It is a curious fact that, though by Darwin's examination, the seeds of the short-styled were more numerous than those of the long-styled, yet the short-styled plants themselves, growing in the woods, etc., do not exceed in number those of the long-styled plants, but that slightly the contrary is the case, at least in our experience. The two sets appear in closely equal numbers. Darwin found that out of 179 flowers, taken from different roots, 83 were long-styled and 96 short-styled. Our own experience is recorded in the enumeration above. In subsequent years, also, the results have been very similar to the above enumeration. This close equality of the plants probably arises from what Darwin notices, that, according to Professor Oliver, "the ovules in the unexpanded and unfertilized flowers of the long-styled are considerably larger than those of the short-styled flower" ("F. Fl.," p. 17). Thus, though the long-styled flowers produce fewer seeds than the short-styled, yet "as their ovules have more space and nourishment for their development," so a larger proportion of their seeds set. By this the close equality of the two sets is maintained.

CHAPTER XXVII

THE TWO FORMS OF HETEROSTYLED PRIMULACEÆ MERELY VARIETIES

Why the two forms of the Primrose and Cowslip exist in Nature is distinctly proved, by the facts produced in the previous pages, not to have been solved by the idea of Darwin, that it was "to ensure cross-fertilization of distinct plants" ("F. Fl.," p. 30); nor is it solved by the alternative form in which Lord Avebury expresses the same idea, that "this condition of the heterostyled *Primulaceæ* is one of the principal modes by which self-fertilization is prevented" ("Fl. and Ins.," pp. 36–38).

"The distinction of the two forms in the *Primulaceæ* has been hitherto considered," Darwin states, "as a case of mere variability" ("F. Fl.," p. 14). The probability that it is nothing more than a mere—though, as we have said, in some species a very persistent—variation, seems necessarily to arise from what has previously been said, and from the following additional facts—

First.—Equal-styled forms are found in species of Primulas. In such forms the anthers and styles are of equal length in the same flowers. Darwin says of the Primulas in general, "some species are homostyled: that is, they exist only under a single form" ("F. Fl.," p. 49); and of the Cowslip, that "with this species and several others, equal-styled varieties sometimes appear." Mr. Scott, of Edinburgh, sent Darwin a Cowslip where the stigmas and

anthers stood on the same level, and "the flowers were highly self-fertile when insects were excluded" ("Cr. and S. F.," p. 235). Of the Primrose, from what Darwin met with in his experiments, he says, "It is therefore probable that an equal-styled form of Primrose might be found on careful search, and I have received two accounts of plants apparently in this condition" ("F. Fl.," p. 225). We have recorded above cases in both forms of equal-styled wild flowers which we met with. But in addition, the four following Primulas produce equal-styled forms: Primula *Sinensis*, *Auricula*, *Farinosa*, and *Elatior* (Oxlip). Of the first, *Sinensis*, Darwin says, "it is often equal-styled"—"the equal-styled variety was not rare" ("F. Fl.," pp. 38, 218, 222).

Secondly.—The one form will produce the other form. "Seeds from the short-styled form of Cowslip (*P. veris*), fertilized by pollen of the same form, produced 14 plants, which consisted of 9 short-styled and 5 long-styled plants" ("F. Fl.," p. 228). And again, "162 plants were raised from long-styled Cowslips, fertilized by their 'own-form' pollen, and these consisted of 156 long-styled and 6 short-styled plants" ("F. Fl.," Table 36, p. 269). The common Auricula of our gardens (*P. auricula*) produced from the short-styled form, fertilized from its "own-form" pollen, 25 long-styled and 75 short-styled offspring ("F. Fl.," p. 269). "Florists," Darwin tells us, "always throw away the long-styled plants of this Auricula, and save seed exclusively from the short-styled form; yet a florist who raises this species in Scotland extensively said that such seeds produced, on an average, one-fourth long-styled flowers" ("F. Fl.," p. 223). Dr. Hildebrand raised from the long-styled form of *P. sinensis*, fertilized by its "own-form" pollen, 17 plants, of which 14 were long-styled and 3 short-styled. From a short-styled plant, similarly fertilized by its own pollen, he raised 14 plants, of which 11 were short-styled

and 3 long-styled ("F. Fl.," p. 217, *n.*). From a short-styled form, fertilized with its "own-form" pollen, Darwin raised 8 seedlings, 7 of which were short-styled and 1 long-styled ("F. Fl.," p. 215).

Lastly.—The two forms, and even the three forms—long-styled, short-styled, and equal-styled flowers—*have been found on the same plant of a Primula.* Darwin says, "With *Primula elatior*, some of the flowers on the same plant have become equal-styled, instead of all of them, as in other species" ("F. Fl.," p. 274). Herr Breitenbach, Darwin tells us, found on 198 plants of the same *P. elatior* (Jacq.)—the Oxlip—growing wild on the banks of the Lippe, a tributary of the Rhine, 894 flowers, of which 467 were long-styled flowers, 411 short-styled, and 16 equal-styled. In 18 cases *the same plant* produced both long-styled and short-styled, or long-styled and equal-styled flowers; and in two out of the 18 cases, long-styled, short-styled, and equal-styled flowers (p. 31). Even Darwin himself, in the case of *P. sinensis*, to which we have already referred, met with different forms, graduated forms, not only on the same plant, but on the same umbel ("F. Fl.," p. 218).

From all the above facts it seems impossible to come to any other conclusion concerning the heterostyled *Primulaceæ* than that the two forms are mere, though in some species very persistent, varieties. Nature herself, from the fact that the two forms, and even the three forms, have been found *on the same Primula*, markedly decides the question. In the face of such facts, we can only repeat the motto—

"Nunquam aliud Natura, aliud sapientia dicit."

The production of one form by the other form is not confined to the Primulas, but extends to other heterostyled *dimorphic and trimorphic* plants.

"From the seeds of the dimorphic short-styled *Pulmonaria officinalis*, carefully self-fertilized," Darwin says, "I

raised 18 plants, of which 13 were short-styled, 5 long-styled" ("F. Fl.," p. 239). The dimorphic *Polygonum fagopyrum* is a remarkable instance of it. "From flowers on the short-styled form, fertilized by its 'own-form' pollen, 33 seedlings were raised which produced 13 long-styled offspring and 20 short-styled ones" ("F. Fl.," pp. 239, 260). On this same plant, the Buckwheat (*Polygonum fagopyrum*), which is grown by our agriculturists, we have seen repeated instances of the short-styled flower on a plant where the majority of the flowers were long-styled. H. Müller notices the same fact. A similar case is recorded by Müller, of *Linum Lewisii*, to that recorded above by Herr Breitenbach concerning *Primula elatior*. "According to Planchon," H. Müller says, "each plant bears flowers of three kinds, one long-styled, one short-styled, and one with styles and stamens of equal length."

"Fert. of Fl.," p. 510.

Ib., p. 149.

The same variability occurs in *trimorphic plants*. Darwin says of the trimorphic plant *Pontederia cordata*, "All three forms of this Pontederia seem to be highly variable" (Preface, "F. Fl.," p. 16). Of *Oxalis acetosella*, Darwin says, "I at first thought that *Oxalis acetosella* was trimorphic. But the case is one merely of great variability" ("F. Fl.," p. 182). From short-styled seed of *Lythrum salicaria*, Darwin raised 12 plants, 1 long-styled, 4 mid-styled, and 7 short-styled forms ("F. Fl.," p. 145). Forty plants raised by Darwin from mid-styled parents, fertilized by pollen from the longest stamens of the short-styled form, "consisted of all three forms, namely, 18 short-styled, 14 long-styled, and 8 mid-styled" ("F. Fl.," p. 203). It is noticeable in this last case that though the seedlings were from a mid-styled flower, the mid-styled seedlings were the fewest in number. "Of the three forms," Darwin says, "the long-styled evinces somewhat the strongest tendency to reappear amongst the offspring, whether both, or one, or neither of the parents are long-styled" (p. 204).

Other instances might be cited of one form producing other forms, but the above sufficiently attest the fact. "I will only add," Darwin observes, "that any single plant of a *trimorphic* species, in a state of nature, produces all three forms" ("F. Fl.," p. 272. The italics are ours).

With such facts before us we may assuredly conclude that all these heterostyled *dimorphic and trimorphic* forms are, like the *Primulaceæ*, mere, though more or less persistent, varieties.

CHAPTER XXVIII

CONCLUSION

When we summarize the above considerations—that the self-fertilized, short-styled Primrose is fully and completely fertile; that there is no evidence in the face of the Primrose that heterostyled flowers stand in the reciprocal relation of different sexes to each other; that the heterostyled flowers, when they become homostyled, produce an abundance of seed when fertilized with their own pollen; that the variation in the stigmatic surfaces, and in the size of the pollen grains in heterostyled dimorphic flowers, is a "positional," not a "functional," variation; and that the two forms by their interchange, the one producing the other, etc., are mere varieties—it is not possible, in reference to Darwin's experiments, to avoid the conclusion that Darwin's terms of "legitimate" and "illegitimate" fertilization are *misapplied*, and that Darwin has not established his theory that reciprocal fertilization is necessary to the full fertility of heterostyled flowers. On the contrary, we are of opinion that the *Primrose* gives unimpeachable evidence, that self-fertilization of heterostyled plants is the *natural* and *legitimate* fertilization, as being fully productive.

If Darwin had only observed, which he unfortunately failed to do, as we have already, in a previous chapter, noticed, that the short-styled Primrose was not subject to cross-fertilization, and yet was fully productive, he would

have perceived at once, when the pistil was elongated to an equal-styled condition with scarcely any sensible influence on its productiveness, that such a variation was merely a "positional," not a "functional," variation. Such a recognition would have saved him a thousand disquisitions about heterostyled plants, by which he endeavoured to prove the contrary. He would never have been led to affirm of the pistil of the very closely allied short-styled Cowslip (*Primula veris*), when it became equal-styled, that "as it varies much in length, one proper to the short-styled form appears to have been elongated, and to have *assumed* at the same time the functions of the long-styled pistil" ("F.Fl.," p. 273). He would have recognized that such functions which it displayed was its own inherent possession. Recognizing the full self-fertility of the dimorphic forms, he would have been open also to the conclusion that the same full self-fertilizing power might be inherent likewise in each of the trimorphic forms. When he met with the cleistogamous flowers of *Oxalis sensitiva*, he could have accepted their testimony to the full self-fertility of these trimorphic forms as the unchallengeable evidence of Nature. Instead of so accepting the evidence unreservedly—*nunquam aliud Natura, aliud sapientia dicit*—he attempts to square Nature to his ideas. He still clung to his theory, and excused his non-acceptance of this natural evidence by saying that he thought "it probable" that the pollen of the cleistogamous flowers was different in function from that of the open flowers growing on the same plant and on the same stem, that "it had been *modified* in power *so as* to act on their own stigmas, for they yield an abundance of seeds" ("F. Fl.," p. 323. The italics are ours). In our opinion, the "naturalist" should have squared his theories to Nature, and not Nature to his theories, and have owned at once that self-fertilization was the *legitimate* fertilization of this trimorphic flower at least, and by analogy of all trimorphic

flowers. Such a conclusion seems naturally to follow, and the more so to ourselves, as we have seen how unreliable and contradictory were the results Darwin obtained in his manifold experiments to prove the contrary.

With respect to the question whether a superior benefit is derived generally in ordinary flowers by cross-fertilization, the evidence, so far as furnished by Darwin's net experiments, in which the inferiority of seedlings raised from seeds of self-fertilized parentage in comparison with those raised from seeds of cross-fertilized parents, cannot be accepted as valid, on account of the unequal conditions to which the former were subjected. The question must be decided, not by artificial observation, as under a net, or in a house, or closed room, or greenhouse, or on garden vegetables, or cultivated flowers, but from the facts which wild nature in the fields and woods provides us with.

The numerous cleistogamic flowers in which all cross-fertilization is absolutely excluded are yet abundantly productive. The number of plants which furnish such flowers is constantly, we are informed, being added to.[1] These flowers give far stronger natural testimony for, than any testimony which can be produced against, Professor G. Henslow's opinion, that "self-fertilization is the legitimate or primæval condition." Thousands upon thousands of flowers of different genera and species, which are never known to be visited by insects at all, are perfectly fertile.

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Professor Henslow has pointed out that "many self-fertilized plants are exceptionally vigorous, such as Groundsell, Chickweed, Sowthistle, Buttercups, and many other

[1] Darwin gives a list of 55 different genera, belonging to 24 Natural Orders, in which cleistogamous flowers are found. Since Darwin's days large additions have been made to their number. Mr. Wallace tells us that Professor Henslow informs him "that many additions have since been made to the list, and that cleistogamous flowers probably occur in nearly all the Natural Orders" ("Darwinism," p. 322).

Henslow's "Self-Fertilization," *Trans. Linn. Soc.* "Floral Structures," p. 315.

common flowers, whilst most plants of world-wide distribution are self-fertilized, and these have proved themselves to be best fitted to survive in the battle of life;" and again, Professor Henslow says, "all regularly self-fertilizing flowers are abundant, and are cosmopolitan."

Mr. Wallace says, "An immense variety of plants are habitually self-fertilized, and their numbers probably exceed those which are habitually cross-fertilized by insects" ("Darwinism," p. 321). This statement is in direct contrast to Darwin's opinion—which was derived almost solely from his misleading net—that "the fertilization of hermaphrodite flowers by insects is incomparably the more frequent case, and that in such cases the wind plays no part" ("F. Fl.," p. 94). Again, Mr. Wallace assures us of some of the advantages of self-fertilization, by the fact that "it is usually the species which have the smallest and least conspicuous flowers which have spread widely, whilst the larger and showy flowered species of the same genera and families which require" (?) "insects to fertilize them have a much more limited distribution" ("Darwinism," p. 323).[1]

"Lay Sermons," p. 258.

We consider that Darwin's use of a close-meshed net, in order to investigate natural operations in fertilization, was most unfortunate. It led Darwin to adopt most untenable theories. Huxley said even in reference to Darwin's theories contained in his *Origin of Species* that "we have to distinguish between the ascertained facts and the theoretical views which the 'Origin of Species' contains." In this case of Darwin's experiments with his net, we have a still further ground for hesitation in accepting his theories; we have to ascertain whether the results which Darwin accepted as natural facts, and on which he founded his theories, are

[1] We have placed a note of interrogation after "require." We think that if Mr. Wallace had said, "which are also subject to cross-fertilization of insects," he would, in a general way, have been much nearer to the facts of Nature.

in reality the facts of Nature at all. That Darwin accepted the results of his experiments as *facts of Nature*, and thence as the basis of his theories, we need only to quote *a few* of the chief instances of the kind, as given by Darwin himself.

"The first and most important of the conclusions which may be drawn from the observations given in this volume—*Cross- and Self-fertilization of Flowers*—is," Darwin says, "that generally cross-fertilization is beneficial, and self-fertilization often injurious. *The truth of these conclusions is shown* by the difference in height, weight, constitutional vigour, and fertility, of the offspring from cross- and self-fertilized flowers" ("Cr. and S. F.," p. 439).

"Scarcely any result from my experiments has surprised me so much as this of the prepotency of pollen from a distinct individual over each plant's own pollen, *as proved* by the greater constitutional vigour of crossed seedlings" ("Cr. and S. F.," p. 399).

"The simple fact of the necessity in many cases of extraneous help for the transport of pollen renders it highly probable that some great benefit is thus gained; and *this conclusion has now been firmly established* by the *proved superiority* in growth, vigour, and fertility, of crossed parentage over those of self-fertilized parentage" ("Cr. and S. F.," p. 372).

"With heterostyled dimorphic species *there are* two females and two sets of males, which differ essentially in their sexual powers" ("F. Fl.," p. 275).

"It has *now been shown* that *Lythrum salicaria* presents the extraordinary case of the same species bearing three females, different in structure and function, and three sets of males; each set consisting of half a dozen, which likewise differ from one another in structure and function" ("F. Fl.," p. 165).

"We *may feel sure* that plants have been rendered

heterostyled to ensure cross-fertilization, for we *now know* that a cross between distinct individuals is highly important" ("F. Fl.," p. 258).

"We *now see* that such sexual differences—the greater or less power of fertilizing and being fertilized—may characterize the coexisting individuals of the same species, in the same manner as they characterize and have kept separate those groups of individuals produced during the lapse of ages, which we rank and denominate as distinct species" ("F. Fl.," p. 277).

"It is *hardly an exaggeration to assert* that seedlings from an illegitimately fertilized heterostyled plant are hybrids formed within one and the same species. *This conclusion* is important, for we *thus learn* that the sterility of the offspring of two organic forms affords no sure criterion of so-called specific distinctness" ("F. Fl.," p. 242).[1]

The points stated in the quotations above as "now known," as "proved," as "firmly established by experiments," etc., have already been discussed, and the reasons given why Darwin's conclusions cannot be received as valid. With respect to the last quotation alone we may make this further remark, that if Darwin's conclusion were a *fact*, all the Primroses which we see in our woods and hedgerows, and all the Cowslips in our pasture fields, would be, with rarest exceptions, hybrids.

The inexorable logic of natural facts is against such a conclusion.[2]

[1] In "Origin of Species," in his chapter on hybridism (pp. 236–239), his erroneous conclusions on heterostyled plants (dimorphic and trimorphic) are recorded in support of his theory there advanced. The italics in all the above-cited passages are our own.

[2] We display in this Note succinctly the eight theories quoted above, which Darwin considered that he had by his net experiments established as *natural facts*. The first three are supposed to be proved from the "crossed seedlings" surpassing in height, etc., the "self-fertilized ones."

Andrew Knight, at the close of the eighteenth century (1799), laid down the law "that in no plant does self-fertilization occur for an unlimited number of generations." It would be impossible to prove this negative. "This law, as a general law of Nature," Müller says, Darwin, in his *Origin of Species*, "placed on broader and surer foundations, and united it intimately with his theory of natural selection" ("Fert. of Fl.," p. 5). Müller also tells us that Darwin, "in his exhaustive researches on the floral contrivances of orchids, had always kept in view as his chief aim the establishment of this law" (Ib., p. 22). In fact, this "chief aim" seems, in a measure, to have warped his judgment in his conclusions concerning the *Orchidaceæ*. His aphorism—Nature *abhors* perpetual self-fertilization—first appeared in his volume on the *Orchidaceæ*. Treviranus objected to Darwin's conclusions—and Müller considers it

1. That cross-fertilization is beneficial, and self-fertilization often injurious.
2. That foreign pollen is prepotent over own pollen.
3. That some great benefit is gained by transported pollen.

} proved from "crossed seedlings."

4. That heterostyled dimorphic plants have two sets of males and two sets of females, which differ essentially in function.
5. That in *Lythrum salicaria* there are three sets of males and three of females, different in function.
6. That plants have been rendered heterostyled to ensure cross-fertilization.
7. That the two forms of dimorphic and the three of trimorphic plants differ from each other in the same manner as distinct species.
8. That seedlings from "illegitimately fertilized heterostyled plants are hybrids."

On the supposed validity of such theories innumerable other theories were based. Hopkins, of mathematical repute at Cambridge in the fifties and sixties, wrote, concerning Darwin's theories in another field of investigation, in *Fraser*, in 1860, "We do not want to know what Darwin believes, or is convinced of, but what he can prove" (Darwin's "Life," ii. 241). So in this field we want proof of Darwin's convictions from *natural* facts, not from *artificial* experiments.

a "well-founded objection"—that "in most orchids, even our native species, the operation of insect-visitors was only concluded indirectly from the structure of the flowers, and had not been directly observed" ("Fert. of Fl.," p. 7).[1]

These "broader and surer foundations," of which Müller speaks, were also supposed to be established by the results which Darwin obtained from his method of experimenting. The aphorism is consequently repeated in his Introduction to *Cross- and Self-fertilization of Plants.* In these experiments, Darwin was possibly led "by his chief aim," unconsciously to himself, to give an undue bias to those results which favoured his theory, and to overlook those which contradicted it. He never expresses any "suspicion" in the repeated cases which he met with of plants producing seeds in those flowers which were in contiguity with the net, whilst the flowers further removed from, or lower in, the net produced none, that this result was brought about by the net itself. He consequently pronounced such plants to be sterile "without insect aid." To this, amongst others, was added Darwin's conviction

[1] We have not noticed in these pages, in any way, Darwin's book, *Orchids and their Fertilization by Insects.* To do this would necessitate undivided attention to individual species, and in a neighbourhood where they grow in considerable abundance. We have, however, but little doubt, from the few species which we have had the opportunity of observing, that any naturalist who could watch them uninterruptedly in their natural habitats, would find that Darwin came to as an erroneous conclusion about their absolutely needing (with one or two exceptions) insect agency for their fertilization, as he did about the absolute need of insect agency in the fertilization of the heterostyled *Primulaceæ*. Professor Henslow tells us that papers by Mr. H. O. Forbes and Mr. H. N. Ridley have been published in the *Transactions of the Linnæan Society* "on the many ways and forms by which self-fertilization is secured in different genera of the *Orchidaceæ*, and that Mr. Forbes discovered that the Orchids capable of fertilizing themselves are not only the most numerous as individuals, but are also the most widely dispersed of the genera to which they respectively belong" ("Flor. Struct.," pp. 253, 318, 319).

that "he had firmly established," as a fact of Nature, "that generally cross-fertilization is beneficial, and self-fertilization often injurious," and which he announced as "proved" by the "greater constitutional vigour of the crossed seedlings." He overlooked the fact of the decided advantage under which they were produced. In the case of the heterostyled primrose, he jumped to the conclusion, when he could produce no sufficient evidence that the flower was visited in the day by the humble-bee, that it must be fertilized by night-flying Lepidoptera. Yet, in support of this view, he had not a shred of evidence. These instances, and particularly the latter one, led Müller to say, "The result of Darwin's investigations of the dimorphic and trimorphic forms was particularly favourable to Knight's law, since it proved that in heterostyled plants not only the occasional crossing of separate flowers, but the regular crossing of separate individuals, was *absolutely necessary for the maintenance of the species*" ("Fert. of Fl.," p. 10. The italics are ours). They also seem to have led Müller to the statement above, that Darwin had placed Knight's law, "as a general law of nature, on broader and surer foundations." We cannot, however, in the face of the real facts, agree with Müller that Knight's law was, by such conclusions, and such experiments of Darwin, placed on "broader and surer foundations."

The Darwinian aphorism, which Darwin well allows, "is perhaps too strongly expressed" ("Cr. and S. F.," p. 8). Nature, as we have seen, in very many instances definitely contradicts. We have seen it distinctly and indisputably contravened in the Primrose and the Arum; generally in the vast Order of the Compositæ; in the almost equally vast Order of the Leguminosæ, in which the pollen is ripe and parted with before the flowers are fully grown, and long before the flowers are opened, conspicuous examples of which are seen in the Common and

Sweet Pea; generally in inconspicuous flowers; and universally in all cleistogamous ones. If Darwin's aphorism were true, we might well ask, Why did Nature, in these cleistogamous flowers, to say nothing of the rest, actually prevent, as far as they are concerned, all possibility of cross-fertilization?

Darwin's use of the net and his method of investigation not only misled Darwin himself as to facts of Nature, but his conclusions drawn from such methods of investigation have misled for an entire generation those of his ablest followers, who, without questioning, accepted his method and conclusions.

H. Müller endorses the conclusion of Darwin (stated above, p. 222), from *Forms of Flowers*, that "it was Darwin's great service *to prove beyond question*, by a long series of patient experiments" (with *Lythrum salicaria*), "that the last barrier that was raised between species and varieties is broken down." He tells us again that Darwin's result from his experiments on dimorphic and trimorphic flowers—to wit, that only the so-called legitimate crossings resulted in full fertility, and that, on the other hand, illegitimate crossings "led to all degrees of diminished fertility and even complete barrenness, and produced offspring which had all the characteristics of hybrids produced by the union of distinct species—broke down the sharp boundary-line between species and variety which had formerly been supposed to be found in the more or less complete sterility of hybrids produced by crossing distinct species."

"Fert. of Fl.," p. 258.

"Fert. of Fl.," p. 10.

If, however, Darwin's conclusions as to dimorphic and trimorphic flowers are unsubstantiated, and his experiments invalid on account of the invalidity of his method of experimenting, the boundary-line between species and varieties still remains unremoved.

In this field of research we cannot suppose it possible

that Darwin's conclusions from his net experiments, and his numerous theories founded upon them, will be abiding. In fact, it involves a decision between results obtained under a net, with sun, wind, and atmospheric influences, generally minimized, and the results as seen in the fields; *i.e.* a decision between *Net-tism* and *Natura-lism*. It needs very little prophetic insight to foretell that the results obtained by the former method will, in the course of another generation, be discarded in favour of the latter. Nevertheless, all naturalists, whether supporters or otherwise of the theories of Darwin here brought under review, are never likely to forget the remarkable, and most unprecedented, impetus to the study of Nature, which his writings, speculations, and genius elicited, and which, as far as the present generation can foresee, will be attached to his name and memory as an abiding inheritance.

As we have questioned the method adopted by Darwin in his experiments, and the theories which he built upon the results, as set before us in his *Forms of Flowers*, and his *Cross- and Self-Fertilization of Flowers*, "we should leave a very wrong impression"—to use the words of Huxley in reference to Darwin's *Origin of Species*—"on the reader's mind if we permitted him to suppose that the value of these works ('that work' in the original) depends wholly on the ultimate justification of the theoretical views which they contain." "Lay Sermons," p. 298.

"If the chief value of a speculation," Mr. Leslie Stephen says, "lies even more in the fermentation which it sets up, than in the results which it finally establishes, no one disputes the enormous importance of Darwin's theories." *Nineteenth Century Review*, December 1890.

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THE END

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